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BULLETIN OF THE TORREY BOTANICAL CLUB

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THE RESPONSE OF ACHRAS ZAPOTA IN LATEX YIELD TO WOUNDING BY THE IBIDEM[1] METHOD OF TAPPING

JOHN S. KARLING

Among the three outstanding characteristics of *Hevea braziliensis* which have made this species the principal source of rubber is its marked positive response in the form of increased latex yield to the stimulus of tapping injury or wounding. When trees are first tapped the yield is comparatively slight, but as a response to daily wounding it increases steadily and eventually reaches a climax. This response as well as a rapid growth rate and the fact that the trees may be bled daily for long periods of time make *Hevea braziliensis* ideal for plantation cultivation and are largely responsible for the vast development of the present-day rubber industry.

In the light of these facts preliminary experiments were made at the start of our Chicle Research Project, under the auspices of the Tropical Plant Research Foundation and the Chicle Development Company, in British Honduras to determine whether or not *Achras zapota*, the principal source of chicle, can be tapped daily and will respond to wounding to the same degree as *Hevea braziliensis*. For these experiments six healthy sapodilla trees were selected near the central camp at Tower Hill, and panels were marked off on the boles for tapping. These trees had a thick, hard, ridged outer bark which was impregnable to the tapping gouges at hand at that time, and in order to tap the trees it was necessary to remove the outer bark completely with a machete. This removal naturally led to marked desiccation of the softer cortical layers during the hot middays, but this drying out was checked by nailing heavy burlap sacks above the panels which could then be let down as soon as tapping and drainage of the latex were completed. These sacks were wetted thoroughly every day, so that the outer layers of the exposed cortex were kept moist.

Tapping began by making an oblique cut or channel at an ascending angle of approximately 40° halfway around the bole, and during the successive daily tappings the lower margin of the initial channel was pared off to reopen the ends of the latex tubes. The gouges used in these initial tests were crude, and it was impossible to remove less than one-eighth inch of bark with each successive paring. For this reason bark consumption in a vertical direction was considerably higher than in tapping *Hevea* (Maas 1926). Daily tapping continued over a period of three weeks and was then

[1] Ibidem, meaning "in the same place" is a descriptive name proposed by Cook (1928) for the present-day method of tapping *Hevea braziliensis*, in which the lower margin of the initial incision is continually pared off during successive tappings.

suspended because of the difficulty of making clean-cut incisions. The results of these preliminary tests in grams of bone-dry chicle were as follows:

Daily yield in grams of bone-dry chicle

Tree no.	Girth	1st day	2nd day	3rd day	2nd week	3rd week
1	3′ 2″	42	0.0	0	0	0
2	2′11″	38	1.80	0	0	0
3	2′10″	26	0.89	0	0	0
4	3′ 8″	52	0.0	0	0	0
5	3′ 1″	35	0.0	0	0	0
6	2′ 9″	40	0.0	0	0	0

The initial yield for the first day is quite high and compares favorably in proportion to tree girth with that of *Hevea braziliensis* as shown by the results obtained by Heusser (1924–1930), Polhamus (1928), Holder and Heusser (1928), Heusser and Holder (1929–1930), Schmole and Prummel (1930), and others. However, with the exception of trees 2 and 3 the yields were negative on the succeeding days. In most panels a few drops of latex accumulated on the pared surface of the oblique incisions if the incisions were accidentally made deeper and uncut latex vessels were severed, but the yield was never of sufficient quantity to be collected. These results suggested at once that *Achras zapota* does not respond to the stimulus of slight daily wounding and cannot be profitably tapped daily in the same manner as *Hevea braziliensis*. As a consequence our time and efforts were concentrated on wound stimulus experiments of another type and on modifying and improving the native method of tapping.

However, in the ensuing years since these initial experiments were performed we felt that the results obtained were not conclusive, inasmuch as the tapping gouges used did not make clean cut incisions. Since that time we have modified the gouge or knife commonly used in tapping *Hevea braziliensis* and made it more suitable to the harder bark of *Achras zapota*. For these reasons it has become desirable during the subsequent years to duplicate our initial ibidem experiments and determine more conclusively the wound stimulus possibilities of the sapodilla tree.

Accordingly, a similar experiment was performed on thirteen trees growing in a cohune palm grove back of the "milpa" at Tower Hill. Young trees with smooth straight boles and a thin outer bark were selected to avoid removal of the outer corky layers before tapping. These trees stand in a dense cohune palm grove bordering Doubloon Bank Savannah where the ground is always damp during the rainy season. Through this grove flows a small sluggish stream which overflows its banks and floods the entire region after heavy rains. As a consequence it is not uncommon to find standing water around the base of the trees for several days after a rainstorm. The dense growth of palms and other trees keep out most of the sunlight and wind, so that relative humidity and tree turgidity (Karling 1934) are quite

high throughout the day. External environmental conditions in this region are thus conducive to maximum yield and sufficiently constant to eliminate most of the effects of transpiration, loss of turgidity, latex coagulation in the incisions, etc., during the period required for tapping and draining of the latex. Tapping began before 5 o-clock a.m. and was usually completed shortly before sunrise. Quite often the work began with the aid of a flashlight, since most of the early dawn light was excluded by the dense growth of palms. With the exception of only two mornings, relative humidity was one hundred per cent during the tapping period and for several hours thereafter.

FIG. 1. Tree 9 showing the manner of opening up the ibidem panels on the first day of tapping. FIG. 2. Tree 1 after 14 vertical inches of bark had been removed.

Each panel was opened approximately three feet above the ground, and the oblique channels extended half-way around the bole as is shown in figures 1–4. The latex was collected separately from each tree in paper cartons, coagulated, dried, and finally analyzed for moisture content. The improved highly-tempered and sharp gouges cut through the outer bark quite easily, severed the latex tubes cleanly, and made perfect oblique channels for the flow of the latex. The depth of tapping extended to within a few millimeters of the cambium, as is shown in table 1, and was kept as uniform as possible throughout the experiment. As in the preliminary tests, the successive daily

tappings were made by paring off the lower margin of the initial channel as sparingly as possible. Bark consumption was thus kept to a minimum, but still not quite as low as in tapping *Hevea braziliensis*. Tapping continued daily without interruption for a period of twelve weeks.

In table 1 are shown the yields for the twelve-week period together with tree girth, bark thickness, initial number of rows of latex vessels, depth of tapping, number of rows of latex tubes severed and remaining, and the amount of bark consumed in vertical inches. All chicle samples were analyzed for moisture content, so that the term "bone-dry chicle" used in this table

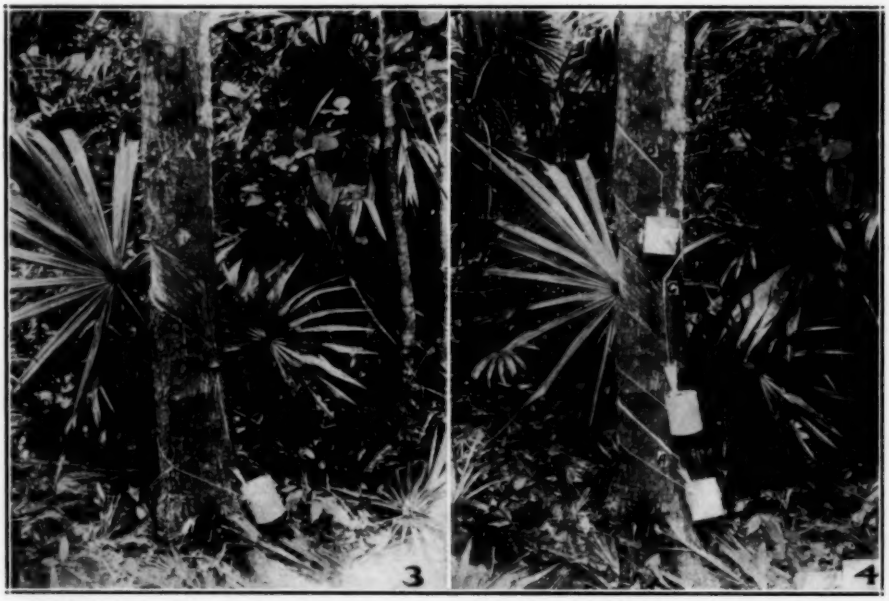

FIG. 3. Tree 5 at the end of the twelfth week of tapping. FIG. 4. Tree 5 showing the position of test incisions A, B, and C in relation to the ibidem panel.

means complete lack of moisture. At the conclusion of tapping a chip of bark with the cambium attached was removed at the upper and lower limits of the ibidem panels as well as directly from the tapped areas. From cross sections of these bark samples the initial thickness of the bark, total initial number of latex tubes, and the number severed were counted and computed for each tree. The thickness of the bark shown in table 1 includes only the cortex between the cambium and phellogen. The outer hard corky layers are omitted in these measurements, since they contain only dead and degenerating latex vessels. The number of rows of latex tubes and the thickness of the bark, however, are not constant throughout the length of the bole but vary considerably in different areas to much the same degree as

Haigh (1928) and others have reported for *Hevea braziliensis*. Within limited areas such as the short ibidem panels, the variations are perhaps less marked. Furthermore, the depth of tapping and consequently the number of rows of latex tubes remaining vary considerably in different parts of the tapped panels. Hence, the figures given in table 1 may not be absolutely constant for the entire panels. They relate only to the particular areas from which the bark samples were taken.

TABLE 1

Girth, thickness of bark, rows of latex vessels, depth of tapping, bark consumption, and yield from 12 trees of Achras zapota tapped by the ibidem method daily for 12 successive weeks

Tree No.	Girth (cm.)	Thickness of bark (cm.)	Initial no. of rows of latex tubes	Depth of bark remaining after tapping (cm.)	No. of rows of latex tubes removed in tapping	No. of rows of latex tubes remaining in untapped bark	Bark consumption in vertical cm.	Yield in grams of bone-dry chicle		
								1st day	2nd day	3rd day to end of 12th week
2	80	1.10	30	.35–.40	20–19	10–11	18.12	15.65	0	0
3	73.12	.57	17	.18–.22	10– 9	7– 8	17.50	9.92	1.42	0
4	58.75	.64	15	.22–.29	12	3	16.87	2.32	0	0
5	60.12	.60	21	.20–.22	16–15	5– 6	16.25	10.64	0	0
6	76.25	.95	24	.25–.35	13–12	11–12	18.12	5.46	.4295	0
7	78.75	.68	27	.15–.20	24–20	3– 4	16.25	9.65	0	0
8	67.50	.69	21	.18	19	2	21.87	5.70	0	0
9	65.62	.65	11	.15–.19	10– 9	1– 2	17.17	9.75	.394	0
10	81.35	.80	21	.25–.35	11	10	19.67	13.05	0	0
11	67.50	.69	21	.20–.30	15–13	6– 8	17.80	6.69	0	0
12	56.35	.55	14	.10–.15	12–11	2– 3	15.62	2.80	0	0
13	73.85	.95	26	.20–.39	18–16	8–10	35.00	10.65	0	0

The results shown in table 1 are conclusive and leave little doubt about the lack of response of *Achras zapota* to the stimulus of daily wounding by the ibidem method of tapping. The yield for the first day is higher in proportion to tree girth than in some reported trees of *Hevea braziliensis* and considerably greater than in *Couma guatemalensis* (Karling 1935). With the exception of trees 3, 6, and 9, however, no latex or gum whatever was secured after the initial tapping throughout the twelve-weeks period although as much as eight vertical inches of bark were pared away in some of the trees. The second-day yield in trees 3, 6, and 9 is probably the result of accidental deeper tapping on that day whereby virgin, uncut latex tubes were severed. The latex system of all trees was continuous to some degree, since in no instances were the deeper-lying latex vessels and cambium severed. As is shown in columns 5 and 7 of table 1, an average of 2 mm of bark and six rows of latex tubes were untouched and intact in each tree at

the conclusion of tapping. As soon as it became evident that no further yield could be secured by the ibidem method of tapping after the first day or two an attempt was made to determine the distance above and below to which the initial incisions had drained the latex supply. Accordingly, in tree 1 (fig. 2) the bark was deliberately pared away more rapidly, so that by the end of twelve weeks fourteen vertical inches had been removed. No latex appeared in the daily incisions until ten vertical inches had been pared away. From then on the amount increased until it was sufficient to cover the lower margin of the oblique cut and flow part of the distance down the vertical groove to the collecting cup.

The results obtained from tree 1 indicate that an incision in the bark of *Achras zapota* drains only a limited area even when part of the laticiferous system is intact and that little or no latex can be secured regardless of the number of incisions which may be subsequently made within such a drainage area. Further proof of this was secured from additional experiments on other trees. At the end of the twelfth week (fig. 3) trees 2–13 were tapped in the same manner with a gouge half-way around the bole 16 inches above and 16 inches below as well as directly opposite the initial incision of the ibidem panel, as is shown in figure 4. These three additional channels are designated as A, B, and C in figure 4 and table 2. As is shown in this figure the latex

TABLE 2

Comparative yields (in grams) of the ibidem panels and channels A, B, and C, "16" above, below, and directly opposite the initial incision

Tree No.	Yields			
	Initial cut	Channel A	Channel B	Channel C
2	15.65	.....	6.68	39.50
3	9.92	.....	7.02	13.55
5	10.64	.....	12.88	13.95
6	5.46	.....	8.25	13.53
7	9.65	6.43	7.07	11.47
8	5.70	4.49	3.60	9.65
9	9.75	.....	6.37	7.80
10	13.05	8.26	16.85	26.60
11	6.69	.....	3.92	6.72
12	2.80	.....	8.68	4.48
13	10.65	3.31	4.77	18.55
Average	8.99	5.62	7.78	14.98

flowed quite freely from these channels, but the yields vary considerably. In all but four of the trees the ibidem panel had progressed so close to the ground by the end of twelve weeks that it was impossible to make channel A at an interval of 16 inches. In the four trees from which the data are complete, the yields from channel A are less than those of the initial incisions of the ibidem panel. Likewise, with the exception of trees 5, 6, 10, and 12,

channel B gave less chicle than the initial one. This suggests that the ibidem panel depleted the latex supply for a considerable distance above and below but not appreciably in a lateral direction. The slightly higher yield from channel C in all but one instance might perhaps be regarded as a response to the stimulus of wounding, but in the light of the wide variations in yield from opposite sides of the same tree which have been secured from other wound stimulus experiments, this seems highly questionable. The general averages in table 2 show that the yield from channels A and B are not very far below those of the ibidem panels. The fact that they yielded any chicle at all, while the ibidem incisions remained almost completely dry after the first day clearly indicates that an incision in the cortex of *Achras zapota* which leaves the laticiferous system intact and continuous to some degree, nonetheless, drains only a limited area. This fact is supported by extensive data from other tapping experiments.

The data from this ibidem tapping experiment confirm the results of the preliminary tests and show without much doubt that the sapodilla tree in British Honduras does not respond to the stimulus of wounding as does *Hevea braziliensis*. These results, however, do not prove conclusively the complete lack or absence of response to injury in *Achras zapota*, but only that the method of stimulation employed on the rubber tree does not produce similar results on the chicle tree. While the many diverse methods of tapping which have been tried up to the present time have failed to show evidence of a wound response, it is not improbable, in light of the positive data from *Pinus*, *Hevea*, and other genera, that this characteristic exists to a lesser degree in the sapodilla tree also and that a type of bleeding may possibly be found which will reveal its presence. Nevertheless, it is quite obvious from the above experiment that *Achras zapota* cannot be tapped profitably daily on a limited panel of cortex.

Whether or not the difference in response between *Hevea braziliensis* and *Achras zapota* is entirely due to differences in type, structure, and continuity of the latex system is not certain. The latex tubes of the former species are more continuous, closely anastomosed, and numerous than in *Achras zapota* (Karling 1929), and this difference may be a contributing factor.

SUMMARY

Tapping experiments on *Achras zapota* in British Honduras involving application of the ibidem method commonly used on *Hevea braziliensis* indicate a lack of response to the stimulus of wounding. The initial oblique incisions in the cortex drain the latex from an area approximately 10 to 14 inches above and below, and daily pairings of the lower margin of the incisions within such areas yield no additional latex. The results obtained show that *Achras zapota* cannot be tapped profitably by the ibidem method

and that the successive incisions in the cortex must be spaced approximately 14 to 16 inches apart to secure the maximum yield per tapping.

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PLANT NUTRITION AND THE HYDROGEN ION—III. SOIL CALCIUM AND THE OXALATE CONTENT OF SPINACH

R. A. SCHROEDER AND WM. A. ALBRECHT[1]

With the fuller recognition of the fact that the increase of hydrogen on the exchange complex, or colloidal fraction, of the soil is the approximate reciprocal of the loss therefrom of plant nutrient cations, the wide range in soil acidity should augur a wide range in the chemical composition of plants. This range may be expected both between plant species and within the same species. Some species reflect the soil nutrient shortage by reduced growth. Others on the same soil do not manifest lowered mass production as the reflection of the soil fertility shortage. They must therefore have lowered concentrations or totals relative to those soil-given nutrients that are deficient for the other plants.

Among the garden vegetables, spinach is a crop that usually makes ample growth over a wide range of soil differences. Its composition in ash constituents is widely variable (6, 2). Its content of oxalate has also been called to attention for its wide fluctuation (5). Because the oxalate is commonly considered a metabolic by-product, the variable amounts of this carbon compound in the crop as related to different levels of soil calcium and to different degrees of soil acidity may shed some light on the interrelations of all these in the plant processes. The dietary importance of spinach as a carrier of calcium, magnesium, and other nutrients, subject to fluctuations caused possibly by soil variations, encouraged the following study of the oxalate content of spinach in relation particularly to the exchangeable calcium in the soil.

PLAN OF THE EXPERIMENT

As a means of controlling the nutrient supply in the substrate, the subsoil of the Putnam silt loam with its high content of colloidal clay was used as a carrier of the exchangeable nutrients. Since not only the clay fraction (1) but also the silt fraction of this soil type are almost inert toward plant growth (3), the coarser fractions were not removed from the finer colloidal ones. The subsoil clay used had an exchange capacity of roughly 28 M.E. per 100 gms. Twelve of the 28 M.E. were hydrogen, twelve were calcium, and

[1] Assistant Professor of Horticulture and Professor of Soils, respectively. Contribution from the Departments of Horticulture and Soils, Missouri Agricultural Experiment Station, Journal Series No. 821.

the balance of the clay's capacity was taken by other elements in minor amounts.

A series of different amounts of calcium was provided by putting specific amounts of it on the clay and using more or less of the treated clay so as to offer 0, 3, 6, 9, and 12 M.E. per plant. The other nutrients similarly supplied in constant amounts included: nitrogen 10 M.E., potassium and phosphate 6 M.E. each, and 3 M.E. each of magnesium and sulfate per plant.

One series was made up by adding oxides and hydroxides of the elements to the acid colloidal clay to give a nearly neutral condition with a final pH of 6.8. The second series was made up by adding them as salts, namely chlorides and sulfates, so that an acid soil at pH 5.2 resulted. These series will be spoken of as the "neutral" and the "acid" series respectively. The clay carrying its supply of exchangeable ions was mixed with quartz sand; put into porous clay pots; planted to a final crop of one plant per pot; and replicated as 40 pots in a single treatment. The amounts of nutrients and of clay per plant were those given in table 1. The plants were grown from Feb-

TABLE 1

Nutrients added to the soil to provide variable calcium levels in "acid" and "neutral" soils

	Nutrients per plant							Clay per plant	Resulting pH
	Ca	N	P	K	Mg	S	Cl		
	M.E.	*M.E.*	*M.E.*	*M.E.*	*M.E.*	*M.E.*	*M.E.*	*gms.*	
"Acid" pH 5.2	0	6	6	6	3	3	2	91.5	5.2
	3	6	6	6	3	3	1	100.0	5.2
	6	6	6	6	3	3	2	125.0	5.2
	9	6	6	6	3	5	3	150.0	5.2
	12	6	6	6	3	9	4	175.0	5.2
"Neutral" pH 6.8	0	6	6	6	3	3	.....	125.0	6.8
	3	6	6	6	3	3	.....	150.0	6.8
	6	6	6	6	3	3	.....	175.0	6.8
	9	6	6	6	3	3	.....	200.0	6.8
	12	6	6	6	3	3	.....	225.0	6.8

ruary 10 to April 15, or a period of 64 days, after which the tops were harvested; dried at 65° C.; weighed; and prepared for chemical analyses.

RESULTS

The growth of the crop as related to increments of exchangeable calcium on the two soils of different degrees of acidity is shown in figure 1. The neutral soil produced slightly more spinach than the acid soil, a mean increase amounting to 7.8 per cent. In its response to calcium, this crop demonstrated the beneficial influence of the increasing amounts of calcium applied in the exchangeable form, regardless of whether the soil was at pH 5.2 or 6.8.

The chemical analyses included determinations of the oxalate, and of calcium, magnesium, strontium, manganese, and potassium. Some of these determinations were made by regular laboratory methods recognized as standard procedures, while some were spectrographic analyses. The results of these chemical analyses, in terms of concentrations, are assembled in table 2. They are given in terms of totals in the crop in table 3.

TABLE 2

Concentrations (percentage) in the crop of spinach when grown at pH 5.2 and at pH 6.8 with variable amounts of exchangeable calcium offered

Soil pH	Calcium offered	Determinations of					
		Oxalate	Calcium	Magnesium	Strontium	Manganese	Potassium
	M.E.	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*	*per cent*
5.2	0	4.87	0.92	0.78	0.0044	0.086	6.54
	3	4.54	0.97	0.78	0.0046	0.093	6.86
	6	5.36	1.21	0.91	0.0053	0.093	6.22
	9	5.31	1.23	1.03	0.0064	0.130	6.28
	12	5.01	1.39	1.21	0.0077	0.225	6.49
6.8	0	3.43	0.53	0.52	0.0020	0.043	5.37
	3	3.98	0.60	0.61	0.0023	0.038	5.88
	6	3.73	0.57	0.57	0.0025	0.038	5.86
	9	4.02	0.59	0.54	0.0025	0.040	6.49
	12	3.35	0.66	0.63	0.0026	0.037	6.92

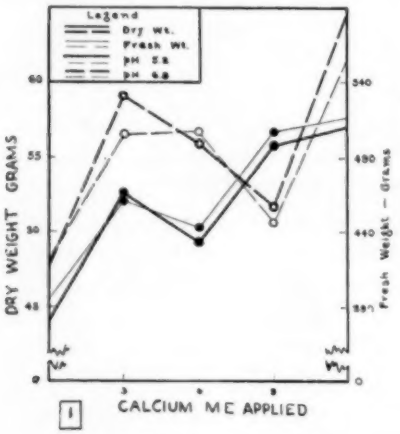
TABLE 3

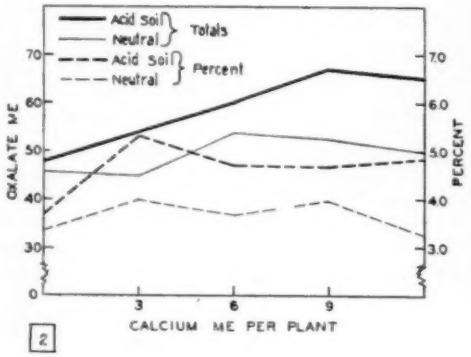
Totals (M.E.) in the crop of spinach when grown at pH 5.2 and at pH 6.8 with variable amounts of exchangeable calcium offered

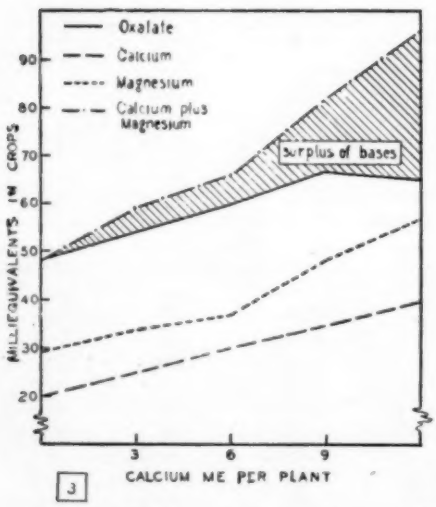
Soil pH	Calcium offered	Determinations of					
		Oxalate	Calcium	Magnesium	Strontium	Manganese	Potassium
	M.E.	*M.E.*	*M.E.*	*M.E.*	*M.E.*	*M.E.*	*M.E.*
5.2	0	48.8	20.3	28.5	0.44	1.38	73.7
	3	54.4	25.7	34.0	0.56	1.80	92.5
	6	60.1	29.8	36.9	0.59	1.68	78.5
	9	67.4	34.5	47.7	0.81	2.66	89.9
	12	65.0	39.7	57.0	1.00	4.67	94.7
6.8	0	37.3	12.8	20.5	0.22	0.75	65.6
	3	54.2	18.1	30.3	0.31	0.84	90.1
	6	47.3	16.1	26.4	0.32	0.78	83.8
	9	47.3	15.2	23.0	0.29	0.75	86.0
	12	48.5	21.2	33.0	0.38	0.87	112.8

One of the outstanding features of the chemical composition of the spinach crop is its higher concentrations and higher total contents of the oxalate,

and of calcium, magnesium, strontium, manganese, and potassium, when grown on the soil originally at pH 5.2 than when on the soil at pH 6.8. In addition, these different concentrations and totals increased, in general, with the increments of calcium in the acid soil, but not so much so on the neutral soil. These increases were apparently associated with increased metabolic performances by the plant as indicated by the larger amounts of oxalate. The







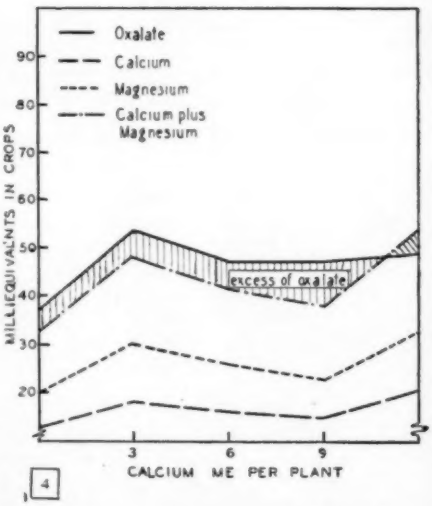


FIG. 1. Weights of spinach (dry and fresh) in relation to the exchangeable calcium applied to the soil at different degrees of acidity. FIG. 2. Concentrations and total amounts of oxalate in spinach as related to the exchangeable calcium in the soil. FIG. 3. Amounts (M.E.) of oxalate, calcium, magnesium, and of the latter two combined, in the spinach crop in relation to the exchangeable calcium in an acid soil, pH 5.2. FIG. 4. Amounts (M.E.) of oxalate, calcium, magnesium, and of the latter two combined, in the spinach crop in relation to the exchangeable calcium in a neutral soil, pH 6.8.

concentrations of the oxalate in the spinach were higher on the acid than on the neutral soil, but not significantly related to the amounts of applied calcium at either pH as is shown in figure 2. That the total amounts of the oxalate in the spinach crop were related to the increments of applied calcium on the acid soil is very evident from the uppermost graph. On the neutral soil the amounts are lower and less closely related to the calcium applications.

Since the oxalate in chemical combination with calcium forms a very insoluble compound, and likewise when combined with magnesium, it will be interesting to note the amounts of oxalate as they are excessive or deficient for complete precipitation of the calcium and magnesium and thus put these two nutrients into possibly inert forms so far as ordinary digestive processes are concerned. These possible relations between the amounts of oxalate in contrast to those of calcium and magnesium combined are best shown in figure 3 for the acid soil and in figure 4 for the neutral soil.

For the acid soil, the combined amounts of calcium and magnesium were increasingly greater than their equivalent in oxalate as more calcium was applied. The calcium treatment may thus be considered as providing both calcium and magnesium in the crop in amounts beyond those which would be precipitated by the oxalate. There would then be available this surplus of these bases, calcium and magnesium, of possible nutritional value even if significant amounts of them had been made insoluble through precipitation by the larger amounts of oxalate. This surplus of bases is relatively larger as more calcium is applied. This is shown by the ratio of the oxalate to the equivalent of calcium, which ratio became narrower, or shifted from 2.4 to 1.6, as more calcium was added to the soil at the outset. It raises the question whether additional offering of calcium might not have given a ratio of one or less, or enough calcium so that it alone might serve to precipitate all the oxalate.

Though the magnesium was applied in constant, exchangeable amount to the soil, the total amounts of it in the crops increased with the increments of calcium applied to the soil. In all cases the magnesium in the crop was larger than the calcium by 25–40 per cent on the acid soil series, and by 50–60 per cent on the neutral soil. But even then in the latter case, or on the neutral soil, the totals of magnesium were less, in general, than those of calcium on the acid soil. Hydrogen ion absence had reduced the calcium intake by the crop more than the intake of magnesium, or the presence of the hydrogen ion activates the calcium for crop use relatively more than it does the magnesium.

The order of these three ions, viz., hydrogen, calcium, and magnesium, in their decreasing degree of adsorption on the clay colloid, may be suggestive. According to this lyotropic series (4) hydrogen is adsorbed to a greater degree than calcium, and calcium to a greater degree than is magnesium.

Accordingly, in the presence of hydrogen to place calcium and magnesium as second and third in the series, the difference in their migrations into the plant is less than when in the absence of hydrogen they are first and second in the adsorption series. Such visualization of these differences may not be the facts, but it is suggestive and helpful in connection with the differences in mobilization of these two bases into the plants in the absence and in the presence of the hydrogen ion on the clay.

In the case of the neutral soil, the combined amounts of calcium and magnesium were not the equivalent of the amounts of oxalate, except where 12 M.E. of calcium were offered per plant. At this high level of calcium offered on the neutral soil, it is important to note that both the oxalate and the calcium in total were just close to the equivalent of that in the crop on the acid soil given no exchangeable calcium. There was then an excess of oxalate which might be expected to precipitate all of the calcium and magnesium and lead us to believe these mineral elements in the crop unavailable for human digestive use. The crop grown under such conditions would not provide these minerals as a vegetable of this type is commonly believed to do.

With the oxalate as one of the plants' metabolic by-products, then, it is evident that the plants were physiologically more active when grown on the acid soil, pH 5.2, than when on the neutral soil, pH 6.8. This is indicated by the higher concentration of oxalate as well as of nutrient cations in the plants on the former than on the latter. This difference in the oxalate amounted as a maximum to 2.0 per cent, and as a minimum to 0.52 per cent, as concentrations in the dry matter. As a mean, the percentage content of oxalate was one-third higher in the former because of the acid condition of the soil. Even though the concentration of oxalate was higher, there was more than enough of the oxalate-precipitating bases taken by the plants from the soil under acid conditions to combine it into the less soluble forms. On the neutral soil, the concentration of oxalate was lower than that in the acid soil by one-fourth, as a mean. But even then, because of the deficiency in the total of the two oxalate-precipitating bases which were less than their equivalent in oxalate, this excess of the oxalate could precipitate and make unavailable some of the calcium contributed to the human digestive mix from other food sources. Thus the spinach might not only be valueless as a calcium contributor, but might even be damaging to the effects by other foods serving this purpose (7).

Whether such views are the actual facts of human digestion, and whether the soil fertility supporting their growth determines the degree to which vegetables are digestive satisfactions or disappointments in our dietary, remains to be more fully determined. They suggest, however, that it might be well to test this hypothesis by means of some assays with smaller animals as help in appreciating the possible situation in human nutrition. Only by

such means can the final facts be fully established even though plant composition differences in relation to fertility variations suggest that human deficiency troubles may find their origin in the deficient calcium and magnesium of the soil on which such vegetables and possibly other products are produced.

SUMMARY

By using the oxalate concentration in the spinach crop as an index of the plants' performances on soils with increasing amounts of calcium under pH of 5.2 and of 6.8, it was shown that the concentration of oxalate in the crop on the acid soil was higher than on the neutral soil. The total in the crop was similarly higher. When the total oxalate was related to the totals of calcium and magnesium it was shown that on the acid soil the amounts of calcium and magnesium taken together were more than the equivalent of the oxalate. With larger additions of calcium to the soil, these two basic cations were present as an increasing surplus over the oxalate.

On the neutral soil the combined amounts of these two cations were not the equivalent of the oxalate except in the case of the soil with the highest calcium application. This soil gave a spinach crop with an excess of the oxalate. Such a result raises the question whether this excess of oxalate may not represent a disturbing condition in the form of calcium deficiency for the plant functions as normal growth.

If the oxalate is considered as removing the two bases, calcium and magnesium, out of reaction in the digestive processes of animals, these results suggest that calcium as a soil treatment for spinach on an acid soil may provide the crop with calcium and magnesium as surpluses over that combined with the oxalate and therefore may contribute some of these minerals of nutritional use. If this soil treatment is applied on a neutral soil, or as a carbonate that should result in neutrality, there is the suggestion that the crop may be so deficient in bases with respect to its oxalate content that this excess of oxalate may not only make the spinach of no nutritional value as a provider of these bases, but may even make it injurious as this excess of oxalate disturbs the calcium coming from other food sources. The composition data of the spinach suggest the need for attention to both the calcium and the magnesium supplies, and to the reaction of the soil growing this crop if the fullest values in terms of its content of these nutrient bases are to be realized.

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THIAMINE PRODUCTION BY ACTINOMYCES VIRIDOCHROMOGENUS

J. ARTHUR HERRICK AND CONST. J. ALEXOPOULOS[1]

During the course of some recent studies on the inhibitory effects of actinomycetes on fungi, six species of *Actinomyces* were grown on liquid media containing sucrose, peptone, and inorganic salts. The mycelium was removed by filtration, the filtrates acidified and then sterilized by autoclaving. Portions of the filtrate from each *Actinomyces* were inoculated with each of nine species of fungi. The degree of inhibition was to be determined by comparing the amounts of fungous mycelium produced in the filtrates with that produced in suitable controls. Owing to the uncertain effects of autoclaving on the inhibitory substances this technique was abandoned for the time being, in favor of growing the actinomycetes and the fungi in apposition on agar (2). Observations made while the filtrate experiments were still in progress, however, revealed that the growth of *Stereum gausapatum* was considerably greater on the filtrate from *Actinomyces viridochromogenus* than on the control medium. The stimulatory effect of this filtrate on *S. gausapatum* was strikingly similar to the effect produced by thiamine on the same fungus (6). The possibility that *A. viridochromogenus* synthesizes and liberates thiamine in culture seemed likely. The present paper deals with the investigation of this problem.

EXPERIMENTAL STUDIES

A liquid culture medium was prepared according to the following formula:

Sucrose	30.0 gm.
Asparagine	1.5 gm.
$MgSO_4$	0.5 gm.
K_2HPO_4	1.0 gm.
KCl	0.5 gm.
$FeCl_2$	0.1 gm.
Distilled water	1.0 liter

The H-ion concentration was adjusted to pH 9 and the medium autoclaved for 10 minutes at 15 lbs. pressure. This caused a precipitate to form

[1] The writers wish to express their appreciation to Dr. H. A. Cunningham, Chairman, Department of Biology, Kent State University, for his encouragement and cooperation in providing research facilities.

which was removed by filtration through filter paper. The medium was then restored to its original volume by the addition of distilled water and the H-ion concentration adjusted to pH 7.3. Several 200-cc. Erlenmeyer flasks, each containing 50 cc. of the medium, were sterilized by autoclaving for 15 minutes at 15 lbs. pressure. One of the sterile flasks was opened and the pH of the medium was found to be still 7.3. One-half of the flasks were then inoculated with a heavy spore suspension of *A. viridochromogenus;* the remaining flasks were reserved to be used later as controls. After 27 days, the *Actinomyces* mycelium was removed by filtration through filter paper, the filtrate restored to its original volume with distilled water, and the acidity adjusted to pH 5.4. The medium was returned to its original flasks in the same amounts as before. The sterile control medium was similarly restored to volume and its pH adjusted to 5.4. The flasks of media were again sterilized by autoclaving for 15 minutes at 15 lbs. pressure. On the following day the flasks of media were inoculated as follows: a) three flasks of *Actinomyces* filtrate and three flasks of control medium were inoculated with *S. gausapatum*, b) three flasks of *Actinomyces* filtrate and three flasks of control medium were inoculated with *Phycomyces blakesleeanus.*

S. gausapatum produced only a scanty submerged growth on the control medium, whereas it produced a heavy surface mycelium on the *Actinomyces* filtrate. The difference between the growth of this fungus on the *Actinomyces* filtrate and on the control medium was even more striking than before because in the inhibition experiments a peptone medium was employed which supports the growth of *S. gausapatum* much better than does the asparagine medium (5).

Within three days after inoculation, *P. blakesleeanus,* which is a rapidly growing fungus, had produced a heavy surface mycelium and an abundance of sporangiophores in the flasks of *Actinomyces* filtrate. In the control medium, there was a weakly developed, submerged mycelium and absolutely no sporangiophores. A week after inoculation, the three cultures of *Phycomyces,* in each of the two media, were filtered through two previously dried and weighed filter papers, respectively, and the dry weight of the mycelium determined. The dry weight of the mycelium of *P. blakesleeanus* produced in three flasks of *Actinomyces* filtrate was 137 mgms., while that produced in three flasks of control medium was 87 mgms.

As a further check, a solid medium, made by adding 2 per cent of "Difco bacto-agar" to the above formula, was prepared and poured into Petri dishes. The plates were inoculated with *A. viridochromogenus* along a two-inch line near one edge of the plate. One week later the same plates were inoculated near the opposite edge with *P. blakesleeanus.* A sparse growth of *Phycomyces* covered the plate in a few days. Near the line of *Actinomyces* growth

there appeared a much more dense mycelium of *Phycomyces* as well as an abundance of sporangiophores.

DISCUSSION AND CONCLUSIONS

It is a recognized fact that *Phycomyces blakesleeanus* cannot grow well without thiamine or its immediate precursors, and further, that the quantity of mycelium produced may be determined by the amount of thiamine available (1). The only thiamine in the original liquid culture medium was the slight trace which is believed to occur as an impurity in the asparagine (3, 8). In the solid medium employed in these experiments there are two sources of thiamine, namely, that provided by the asparagine, and that which occurs in the "Difco bacto-agar" used as a solidifying agent (4). The pronounced growth and sporangiophore production by *P. blakesleeanus* in the medium which had previously supported *A. viridochromogenus,* in contrast to the poor growth and absence of sporangiophores in the control medium, is offered as proof that *A. viridochromogenus* produces significant amounts of thiamine, or its immediate precursors, in culture.

It is of interest to note that Mackinnon (7) has recently demonstrated that *Actinomyces albus* is also able to produce thiamine in culture media. Further investigations are now in progress to determine whether or not thiamine production is a general property of the genus *Actinomyces.*

SUMMARY

Actinomyces viridochromogenus was grown on an alkaline liquid medium. The cultures were then filtered, the filtrate acidified and autoclaved. This filtrate was found to support a heavier growth of *Stereum gausapatum* than similar media which had not previously supported *A. viridochromogenus.* Similar, but more pronounced results were obtained when *Phycomyces blakesleeanus* was substituted for the *Stereum.* When *P. blakesleeanus* was grown on agar plates previously inoculated with *A. viridochromogenus, Phycomyces* produced a much denser mycelium and a crop of sporangiophores in the vicinity of the *Actinomyces* colony. Since the growth of the *P. blakesleeanus* is a recognized assay for thiamine it is concluded that *A. viridochromogenus* produces thiamine in culture.

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AN ANALYSIS OF THE WOOD OF THE THREE COMMERCIAL SPECIES OF WHITE PINE

EDWIN B. MATZKE AND ROBERT L. HULBARY

In the course of work on the lumber of the three white pines of commerce —*Pinus strobus*, northern white pine, *P. monticola*, western or Idaho white pine, and *P. lambertiana*, sugar pine—it was necessary to distinguish microscopically between the wood of these species. An examination of the literature failed to disclose any very definite and infallible criteria which could be used, and therefore a brief treatment of the results of investigations on the microscopic characters of the wood is herewith presented, together with some broader considerations of the interrelationships of these species.

The similarity in the wood of these pines is almost to be expected, since the trees have so much in common; in fact, the western white pine has been considered a variety of the northern. All of them are tall and straight five-needled pines, having needles of nearly the same length, and similar cones. The latter are long-stalked, comparatively elongated, and rather thin-scaled, the scales are unarmed, and the seeds have relatively large wings; the seeds of all of them mature in the second season. *Pinus strobus* is usually distinguished from the others by its more delicate and slightly longer leaves and by its somewhat shorter cones, while *P. lambertiana* differs from *P. monticola* especially in having larger cones and slightly coarser needles. In internal leaf structure, *P. strobus* and *P. monticola* are similar in having thinner-walled subepidermal cells, while *P. lambertiana* has thicker-walled cells beneath the epidermis and usually around the resin ducts (Coulter and Rose 1886; Sargent 1897). Although there are constant differences between these species, they are fundamentally similar and obviously related. *Pinus strobus* covers a wide area in eastern North America; *P. monticola* is found in northern Montana and Idaho and farther west from British Columbia into California; *P. lambertiana* extends from Oregon southward into Lower California (Sargent 1897, 1933; Britton 1908).

On the basis of wood characters, Record (1934) groups *Pinus strobus* and *P. monticola* together in his key and states that the lumber of the latter is "ordinarily not distinguishable" from that of the former. The essential similarity of the wood of these three species is also evident from a study of the table of characters given in the article by Phillips (1941). In dealing with minute features, Brown and Panshin (1940), in their excellent book, separate these three pines on the tangential diameter of the longitudinal resin canals and on the number and general character of the pits leading

from the ray parenchyma cells to the spring tracheids. They characterize the ray parenchyma pits of *P. lambertiana* as "large (window-like)," "rounded and more or less widely spaced"; those of *P. monticola* are described as "large (window-like)," "more or less angled and occupying most of the back wall"; in *P. strobus* they are called "large (window-like)," "more or less angled and occupying most of the back wall." Penhallow (1907) describes the ray parenchyma pits of *P. lambertiana* as "very large, oval"; those of *P. monticola* as "large, oval or oblong or lenticular"; those of *P. strobus* as "very large, oval, or lenticular." Larsen and Woodbury (1916) have also made careful comparisons of *P. strobus*, *P. monticola*, and *P. lambertiana*. They caution judiciously that identification of the wood by means of either gross or minute characters should rest on comparison of all available features, and not on any one alone. Anatomical differences between groups of species of pines are given by Rol (1932); using the details of the ray tracheids and of the ray parenchyma pits, he places *P. strobus* and *P. monticola* both in the section *Strobus*, without listing further distinguishing features. *P. lambertiana* is not included in his scheme. The general wood anatomy of the pine, especially of *P. strobus*, is taken up by Jeffrey (1917). Spaulding and Fernow (1899) have considered *P. strobus* in detail. General wood characters of all the commercial pines are thoroughly discussed by Hall and Maxwell (1911).

The gross characteristics of the wood of these three pines show striking similarities. In each species the wood is rather soft, straight-grained, fairly light in color and in weight, and the transition from spring to summer wood is gradual. The resin canals extend in both longitudinal and transverse directions, and they are numerous and easily visible to the naked eye. Sugar pine is distinguished from the other two species, macroscopically, by its somewhat coarser texture, its more conspicuous and often dark brown resin ducts, by the sugary exudation often found in newly cut wood, by its stronger odor, and by its slightly different color. Idaho white and northern white pine wood vary in color from nearly pure white to reddish brown; sugar pine is not so nearly white in color, nor is it ever quite so reddish brown as the other two. Idaho white pine wood can hardly be distinguished from that of the northern white pine on gross characters, though the color is often somewhat lighter in the former.

The more minute features of the wood of these three pines, as revealed by microscopic examination, are also similar. The general characters of the tracheids, of the resin ducts, the absence of dentate ray tracheids, and the general similarities of the pits of the ray parenchyma cells, as contrasted with those of other species of pine—all show a striking likeness in these species. However, Brown and Panshin (1940) as well as Larsen and Woodbury (1916) point out that the diameter of the resin ducts is greatest in

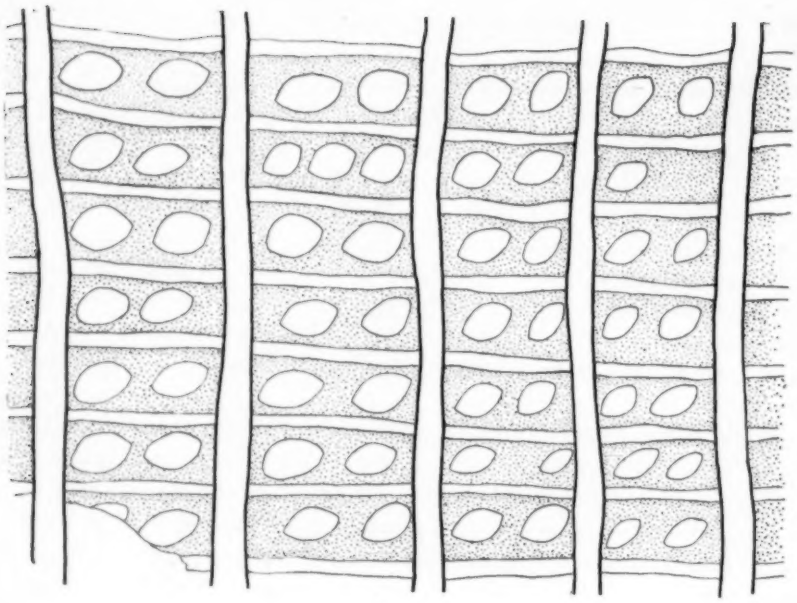
P. lambertiana and least in *P. strobus*, and they also indicate, in somewhat general terms, that there are differences in the pits on the radial walls of the pith-ray cells. Brown and Panshin further state that the average diameter of the tracheids is greatest in *P. lambertiana* and least in *P. strobus*, though in this respect the difference between *P. lambertiana* and *P. monticola* is slight.

In the present study mature wood and sections of wood obtained from four different sources were used for comparison. The results are based on large numbers of sections. They do not include investigations of twigs, of the earliest annual rings, of roots, or of trees growing under unusual conditions.

A microscopic study of these three species shows that one of the most reliable differences in minute structure is found in the pits of the ray parenchyma cells. These pits, which occur on the walls of the ray parenchyma cells in contact with the radial walls of the tracheids, vary in size, in shape, and in distribution. Figures 1, 2, and 3 are radial sections of the wood of *Pinus lambertiana*, *P. monticola*, and *P. strobus*, respectively. The vertical lines represent sections longitudinally through the tracheids, while the horizontal lines show the ray parenchyma cells. A ray tracheid is also shown in figure 2. All the drawings were made from spring tracheids.

It is obvious from figure 1 that each ray parenchyma cell in *P. lambertiana* usually has two pits per tracheid. However, although this is rather generally true, there may be only one, as frequently happens also in the narrow tracheids of the summer wood, or there may be three or occasionally four in wide tracheids of the spring wood. Brown and Panshin and Larsen and Woodbury speak of these pits as round, or rounded, but this description seems hardly adequate. In the spring wood they are somewhat lemon-shaped, often more or less apiculate both above and below, along a diagonal axis, as shown in figure 1. Although this shape of the pits is not invariable, it very generally occurs, and it seems to be the most reliable microscopic character in identification of the species. These pits are somewhat smaller, both actually and relatively, than in the other two species. They are also more uniform in size and more regular in outline than in *P. monticola* and *P. strobus*. In the summer wood they are distinctly narrowed along the diagonal axis.

From the standpoint of minute wood anatomy, the structure of *P. monticola* comes close to that of *P. lambertiana*. Here again there are usually two pits per ray parenchyma cell for each tracheid, but there may be just one, especially on the narrower tracheids, or there may be more than two, though usually there are not more than three. In this species the pits vary greatly, as is shown in figure 2. Some of them are strongly suggestive of those characteristic of *P. lambertiana*, though usually they lack the suggestion of the apiculate feature found in the latter species. Many of the pits of *P. mon-*



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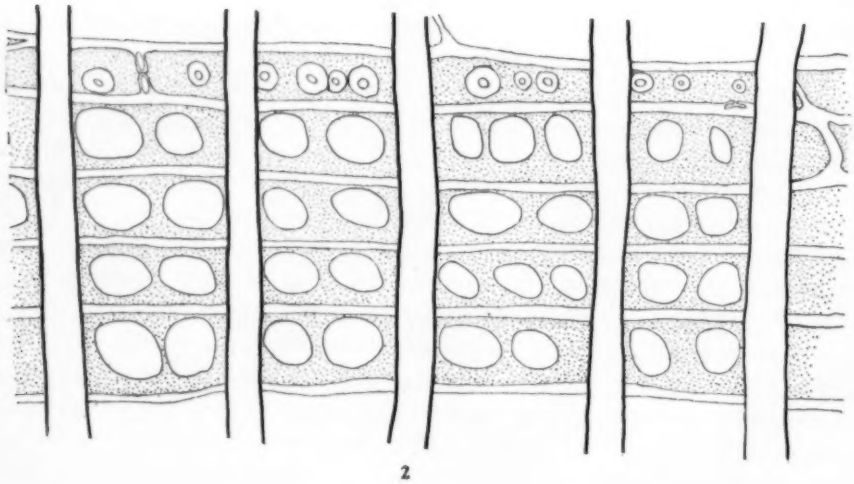

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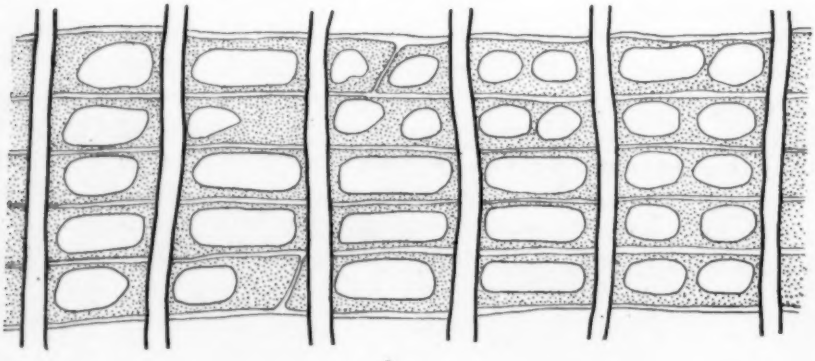

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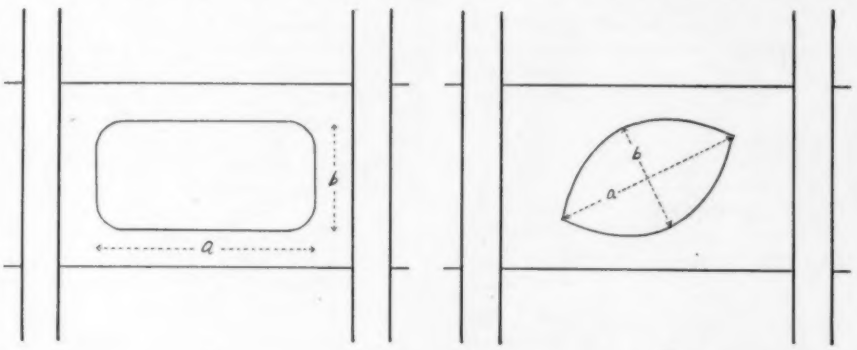
ticola are rounded, though usually somewhat irregularly so, and some of them are distinctly oval. If there is just one pit per tracheid, it may be distinctly flattened horizontally and rounded at the ends. The pits of *P. monticola* normally occupy more of the available wall space than those of *P. lambertiana*, and they are somewhat larger; they lack the uniformity of orientation so characteristic of the latter species.

In the wood of the northern white pine, *P. strobus*, the diameter of the tracheids of the spring wood is normally less than in the other two species.



4 5

FIG. 4. Diagram of an oblong ray parenchyma pit. FIG. 5. Diagram of an elliptical ray parenchyma pit. The axes that were measured for tables 1 and 2 are indicated by the dotted lines, *a* and *b*.

Often there is a single large oblong pit for each ray parenchyma cell per tracheid, as shown in figure 3. Not uncommonly there are two such pits, however, and occasionally there may be three. If there are two or three pits, they are not so elongated, but more rounded; the suggestion of an apiculate feature is rarely present. These pits are larger than those of the other two species, and they occupy a greater proportion of the available wall space. On the basis of these pit characters, *P. strobus* is distinguished from the others.

Data to illustrate these features are given in tables 1, 2, and 3. The pit measurements of table 1 were made with an ocular micrometer. The length of elliptical pits was taken along the long axis, as indicated by *a* in figure 5, regardless of whether this axis was horizontal or oblique; the short dimen-

Explanation of figures 1–3

FIG. 1. Longitudinal section of the spring wood of the sugar pine, *Pinus lambertiana*, showing the ray parenchyma pits. The pits here are lemon-shaped, some more or less apiculate, usually two per ray crossing. ×370. FIG. 2. Longitudinal section of the spring wood of the Idaho white pine, *P. monticola*, showing the ray parenchyma pits. The pits here are mostly somewhat irregularly rounded or slightly oblong, usually two per ray crossing. A ray tracheid is shown above. ×370. FIG. 3. Longitudinal section of the spring wood of the northern white pine, *P. strobus*, showing the ray parenchyma pits. The pits here are mostly oblong, often one per ray crossing. ×370. Pits in the upper and lower walls of the ray parenchyma cells are not shown in these illustrations.

sion, *b*, was taken at right angles to the long one. Oblong and rectangular pits were measured along the horizontal and vertical axes. The pits were chosen at random. These measurements are significant as indicating relative rather than actual dimensions. It would be possible, for instance, to choose pits of *P. lambertiana* with dimensions larger than those of chosen pits of *P. strobus*. In no case were measurements made from summer tracheids.

An inspection of table 1 indicates that the pits are longest in *P. strobus* and

TABLE 1

Dimensions of ray parenchyma pits on radial walls of tracheids

	P. lambertiana Average in μ per pit		*P. monticola* Average in μ per pit		*P. strobus* Average in μ per pit	
	Length	Width	Length	Width	Length	Width
2 pits per ray crossing	17.5 (200 pits)	12.0	15.1 (300 pits)	15.0	19.0 (200 pits)	15.9
1 pit per ray crossing	21.7 (200 pits)	13.6	21.5 (300 pits)	15.0	31.2 (200 pits)	14.5
Totals	19.6 (400 pits)	12.8	18.3 (600 pits)	15.0	25.1 (400 pits)	15.2

narrowest in *P. lambertiana*. This is true when there are two pits per ray crossing, and also when there is only one. *P. monticola* is more or less intermediate. The average length and width of pits of *P. monticola* are practically equal when there are two per ray crossing.

In order to analyze the character of these pits further, the length and width of two hundred of each species were measured, and a record was kept of the approximate shape of each of these—i.e., whether they were oblong, circular, or elliptical. The area of each of the oblong pits was calculated by multiplying length by width; the area of the circular ones was calculated from the formula πr^2; and the area of the elliptical ones was calculated from the formula of the area of an ellipse, πab. These results were then assembled, and the average area per pit, in sq. μ, is given in table 2. In area, as well as

TABLE 2

Area of ray parenchyma pits on radial walls of tracheids

	P. lambertiana Average area in sq. μ per pit	*P. monticola* Average area in sq. μ per pit	*P. strobus* Average area in sq. μ per pit
2 pits per ray crossing	165.4 (100 pits)	176.4 (100 pits)	276.2 (100 pits)
1 pit per ray crossing	269.0 (100 pits)	278.7 (100 pits)	448.8 (100 pits)
Totals	217.2 (200 pits)	227.6 (200 pits)	362.5 (200 pits)

in linear dimensions, the pits of *P. strobus* are the greatest, those of *P. lambertiana* are the least, while those of *P. monticola* are intermediate.

Next, 2,175 pits of these three species were examined with a view to determining how many of each were elliptical, how many circular, and how many oblong or rectangular. The results are summarized in table 3. It is evident

TABLE 3

Shape of ray parenchyma pits on radial walls of tracheids

	P. lambertiana					
	2 pits per ray crossing (442 or 61.9%)		1 pit per ray crossing (272 or 38.1%)		Total (714)	
Oblong	63	14.3%	115	42.3%	178	24.9%
Circular	37	8.4%	0	0.0%	37	5.2%
Elliptical	342	77.4%	157	57.7%	499	69.9%
	P. monticola					
	2 pits per ray crossing (494 or 67.3%)		1 pit per ray crossing (240 or 32.7%)		Total (734)	
Oblong (and square)	314	63.6%	208	86.7%	522	71.1%
Circular	75	15.2%	6	2.5%	81	11.0%
Elliptical	105	21.2%	26	10.8%	131	17.9%
	P. strobus					
	2 pits per ray crossing (450 or 61.9%)		1 pit per ray crossing (277 or 38.1%)		Total (727)	
Oblong	293	65.1%	271	97.8%	564	77.6%
Circular	45	10.0%	1	0.4%	46	6.3%
Elliptical	112	24.9%	5	1.8%	117	16.1%

that those of *P. lambertiana* are more commonly elliptical than any other shape, while those of *P. strobus* are usually oblong, and *P. monticola* again is intermediate. Many of the pits of this last species, especially when there were two per ray crossing, were nearly or quite square. Many of the elliptical pits, particularly of *P. strobus*, were not diagonally oriented, and they gave no suggestion of the apiculate feature.

Comparing the parenchyma pit characters of *P. lambertiana* and *P. strobus*, it is obvious that there are distinct differences, as has been pointed out. Microscopically these two species, though fundamentally similar, could hardly be confused. It would be difficult to conceive of a more perfect series of intergradations in pit characters between these two species than is offered by *P. monticola*. In this last species some of the pits suggest *P. lambertiana* and some suggest *P. strobus*. However, the majority of the pits are not the

same as in either of those two species, but are intermediate in character between them. It is thus usually possible to distinguish *P. monticola* by the use of these microscopic wood characters. The admonition of previous writers that all the microscopic characters ought to be used for identification should be emphasized again; numerous sections should be studied, since different parts of the same wood show considerable variation, even in small pieces.

These microscopic distinctions are not merely biological and academic, since the lumber also shows differences in standard tests. According to Markwardt and Wilson (1935), the wood of *P. monticola* is the "strongest" in certain ways, though this tree is normally the smallest of the three.

On the basis of external leaf characters, *P. lambertiana* and *P. monticola* obviously are more closely similar to each other than to *P. strobus*. The gross cone features also form a series, with *P. lambertiana* and *P. strobus* at either end. Macroscopically, the woods of *P. strobus* and *P. monticola* are hardly distinguishable from each other, though they can be told, generally, from that of *P. lambertiana*. The microscopic wood characters, on the other hand, form a beautiful series with *P. strobus* distinct at one end, and *P. lambertiana*, also distinct, at the other. The wood of *P. monticola*, as shown above, contains an almost imperceptible series of intergradations microscopically between the two; possibly it is a bit closer to *P. lambertiana* than to *P. strobus*.

The distribution of the species fits in well with the microscopic features of the wood, for *P. strobus* is found in eastern North America, *P. lambertiana* in the far west, and *P. monticola* somewhat between, although partially overlapping the range of *P. lambertiana*.

Both Britton (1908) and Sargent (1933) treat these three species in the same sequence—namely, *P. strobus*, *P. monticola*, and *P. lambertiana*—and that is not just fortuitous. Nuttall (1849) considered *P. monticola* as a variety of *P. strobus*. The microscopic wood characters strongly support the sequence of Britton and Sargent, and they emphasize the fact that *P. monticola* is a species in many ways intermediate between the other two, but distinct nevertheless. This should not be construed, however, as indicating that this is a definite, closed series. There are other related species, both in western North America and in Asia, which probably form a part of this series. A study of these forms is at present under way.

Bailey (1910) has shown how the larger ray parenchyma pits may be derived from smaller ones. Bailey and Faull (1934) have pointed out the variations that occur in the microscopic features of *Sequoia*, and more recently Bannan (1941a, 1941b, 1942) has dwelt on this same subject for a number of conifers, more especially the genera *Thuja* and *Juniperus*, but others as well.

In this connection it should be noted that in the present study mature wood only was examined. An intensive analysis of twigs, of roots, and of injured members might well bring out differences not here recorded. It would be of interest to study these species growing under varied conditions and trying environments. Such work should throw further light upon the interrelationships of these forms.

SUMMARY

The pits of the ray parenchyma cells in contact with the tracheids are described in detail for the three white pines of commerce. As shown in figures 1, 2, and 3, they are large and oblong in *Pinus strobus*, somewhat smaller and lemon-shaped in *P. lambertiana*, and intermediate in *P. monticola*. In ray parenchyma pit characters the last species is a little closer to *P. lambertiana* than to *P. strobus*. In other features, both gross and microscopic, *P. monticola* also is intermediate between the other two.

The series thus formed on the basis of wood characters coincides with that appearing in the manuals and conforms with the distribution of these three species in nature, though other species undoubtedly also form a part of this series.

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CORNUS SERICEA L. (C. STOLONIFERA MICHX.)

F. R. FOSBERG

There has been little agreement among the treatments of the small complex of forms centering around what has been called *Cornus stolonifera* Michx. By some workers each discernible element has been considered a separate species. Others have regarded some of the groups as varieties of those which they have termed species.

Enough specimens have been accumulated in the herbaria in Washington, Philadelphia, and New York to enable one to get a fair idea of the diversity and distribution of these forms. An examination of some hundreds of sheets, variously named *Cornus stolonifera*, *C. baileyi*, *C. pubescens*, *C. instolonea*, *C. californica*, *C. interior*, *C. occidentalis*, *C. nelsoni*, etc., has convinced me that the whole variable population is best regarded as a single species, and that this might not be termed even a collective species by some conservative students. Current treatments seem mostly to be the result of a definite effort to recognize species, no matter how indistinguishable they are.

With the exception of some alleged differences in the shape of the stone in the fruit, the characters which have been used to separate the forms lie in the color of the twigs, the abundance and distribution of two types of hairs and the prominence of the veins on the lower leaf surface. Whether or not the plant is stoloniferous is often mentioned, but this is ordinarily indeterminable in the herbarium, except as rarely noted by the collector.

It is on the basis of the hair types that the different forms are commonly recognized, and fairly easily distinguished. Actually, these differences are so slight and so inconstant that they cannot represent very fundamental genetic changes. A single allelomorphic series of genes might well be responsible for these differences. The geographical distribution of the plants differing by these characters is such as to indicate merely a variation in composition of the local partial populations from place to place in a single large population, giving evidence of some environmental selection.

The differences in the size, shape, and sculpturing of the stone, though conspicuous, cannot be ascribed much importance. There is too much local variation, even within one inflorescence. The only stone character which I consider of any consequence in this species is the presence or absence of sculpturing, usually in the form of longitudinal ridges, on the lateral faces of the stones. This seems to be definitely associated with the plants which have been called *C. californica* and *C. pubescens*.

Fruit color is variable. Usually it is white, but occasionally it is pale blue.

In flower size there seems to be some significant variation. In eastern and northern specimens the range of variation in length of petals is ordinarily 2 to 3 mm. Much of the western material, especially that from California, varies around 4 mm., some even reaching 5 mm.

From the foregoing, it seems that the complex can be considered merely an aggregation of forms, based on the differences in pubescence. Even though some of these are more or less restricted in their distribution, my opinion is that genetically they do not merit the rank of *varietas*. However, on the basis of the larger flowers and the sculptured stone the two Pacific forms may be considered to represent, together, a separate subspecies, here called ssp. *occidentalis*.

The division of the species thus into two subspecies, each with several poorly localized forms, seems to be nearer to a representation of the actual diversity than any other arrangement that I know of. It might well be argued that even so the group is segregated too finely. Certainly the diversity is no greater than that within many species which have never been divided in any way.

This scheme leaves a number of plants in the western part of the range which do not fit either subspecies. It may be assumed that the presence, in western specimens, of any of the following characters—spreading hairs, large flowers, or sculpturing on the faces of the stones—is an indication of some ssp. *occidentalis* heredity. Where these characters are all or mostly present, the plant may be considered to belong to that subspecies. Where a furrowed stone or large flowers are found in eastern specimens, I would suspect past crossing with the closely related *C. amomum* Mill. This apparently happens very rarely.

Unfortunately, in spite of the discussions by Farwell (Rhodora **33**: 68–72, 1931) and Rickett (Rhodora **36**: 269–272, 1934), the correct epithet to be applied to this species has not been settled. Both of the above authors find that the name *Cornus sericea* L. applies, with the exception of the Plukenet reference, to what has been known as *C. stolonifera* Michx. That this is true is obvious from a scrutiny of the original description which is detailed enough. The only discrepancy is in the color of the fruit, which probably came from the Plukenet reference, though there are blue fruited forms of the plant under discussion (cf. *Fernald 305* [US]). In addition to this, both of the above writers refer to the specimen in the Linnaean Herbarium of *C. sericea* as being without doubt what has been called *C. stolonifera* Michx. In Jackson's index to the Linnaean Herbarium this specimen was listed as of unknown date, but in the original publication of *C. sericea* there is the abbreviation "H. U." which I take to mean that the plant was growing in the garden at Upsala at the time the description was written. It is possible that the fruits had not matured at the time the description was written, so

the color may have been taken from the Plukenet reference, or the plant may have been a blue-fruited form. In the absence of better evidence to the contrary, the specimen in the Linnaean Herbarium must be accepted as typifying the species, giving *C. sericea* L. (1771) clear priority over *C. stolonifera* Michx. (1803).

Farwell avoided the logical consequence of this view by proving, to his satisfaction, at least, that *C. amomum* Mill. (1768) should properly apply to this species. After reading what Miller says of his *C. amomum* I cannot agree to this. Rickett, after demonstrating conclusively that *C. amomum* is correctly applied in its traditional sense, faced with the necessity of replacing *C. stolonifera* with *C. sericea*, showed that it had commonly been regarded as a synonym of *C. amomum*, as interpreted by Willdenow. This being the case, he suggested placing *C. sericea* on the list of *nomina ambigua*.

This disposition I can scarcely accept. In the first place, there is no provision in the International Rules for a method of placing things in this, as yet, non-existent list. Secondly, if this list is to be used for the disposal of any name which upsets a long established usage, it merely becomes an application of the idea of *nomina specifica conservanda* under a different name. This principle was decisively rejected by at least two congresses. If all names about which there has in the past been uncertainty or confusion are to be placed in the list of *nomina ambigua* the number of familiar names that will fall should make anyone stop and reconsider. In this case there seems scarcely even much actual confusion, since in recent years *C. sericea* has only been thought of as a synonym. The translation "silky cornel," which has been applied somewhat to *C. amomum*, is unfortunate, but is the logical result of the practice of manufacturing common names by translation of scientific names. The appellation "silky" seems to me to apply much more aptly to the appressed pubescence of the plant under discussion than to the spreading or woolly, often rusty pubescence of *C. amomum*. The consequent confusion attendant on the change of one familiar name seems to me much less than that which would follow a precedent such as placing *Cornus sericea* L. in the list of *nomina ambigua*. If no new combinations were to be made here, it would be simple, of course, to express my opinion and then continue to follow usage, leaving it to a monographer to do something about it. Since there are new combinations, I feel that it is advisable to make them under *C. sericea* L.

Unhappily, this decision was reached after I had annotated a considerable number of specimens with the appropriate epithets under *C. stolonifera*. Those combinations are to be regarded as unpublished herbarium names, which I hope no one will feel called upon to dig up and insert into the literature.

The herbarium abbreviations used with the occasional citations are those

of the last list of standardized abbreviations published in Chronica Botanica (**5**: 143–150, 1939; **6**: 377–378, 1941).

CORNUS SERICEA L., Mant. **2**: 199, 1771. *Cornus stolonifera* Michx. Fl. Bor. Am. **1**: 92, 1803.

(For detailed synonymy applying to the species, see that under the subspecies and formae.)

The distribution of this species in eastern North America lies almost entirely within the glaciated region. In the West it extends along the Rocky Mountains to Chihuahua, Mexico, through the Great Basin to the mountains of Arizona, and on the Pacific Coast from Alaska to San Diego County, California. Its northern limits have not been determined, but it is known from Newfoundland, Keewatin, Mackenzie, the Yukon Valley, and coastal Alaska.

Its closest relatives seem to be *Cornus alba* L. of northeastern Asia and *C. amomum* Mill. of the eastern United States. *C. alba* differs in having the stone longer than broad, and acute at each end. *C. amomum* differs in its brown pith and in having the stone subglobose and ribbed. *C. hessei* Koehne, of northeastern Asia, which I do not know, may be even closer to *C. sericea*.

A key to such a variable and intergrading series of forms is rather useless, as it will necessarily not work with those individuals which partake of the characters of two or more forms. However, the following will make possible the identification of flowering or fruiting material of a large majority of the plants of this species.

1. Petals 3.5–5 mm. long, stone with lateral faces sculptured, pubescence spreading except sometimes on inflorescence branches (ssp. *occidentalis*).
   2. Inflorescence with spreading hairs even on minor branches ..... f. *occidentalis*.
   2. Inflorescence with spreading hairs on peduncle only (rarely on large divisions) ..... f. *californica*.
1. Petals 2–3 mm. long, stone with lateral faces smooth, pubescence all or at least partly strigose (ssp. *stolonifera*).
   3. Under side of leaves with spreading or woolly hairs ..... f. *baileyi*.
   3. Under side of leaves strigose, except sometimes near midrib.
      4. Peduncle strigose, young twigs glabrous or thinly strigose ..... f. *stolonifera*.
      4. Peduncle with spreading hairs, young twigs tending to be woolly or densely appressed pubescent ..... f. *interior*.

Specimens are not usually cited, as they would take up much space and this discussion is not intended to be monographic. A selection of a few representative ones would perhaps give a false idea of the distribution of the forms. The synonymy cited for categories above *forma* is just that necessary to establish priority, except that the horticultural varieties have only been assigned to subspecies. This is because of uncertainty about the final disposition of these cultivated forms, and because I have not seen authentic material of most of them. For the forms all synonyms known to me which are based on wild plants are placed, some, of course, tentatively pending availability of types. Those names which have elsewhere been cited as synonyms but which are merely misapplications of names of other plants are not included.

CORNUS SERICEA ssp. **stolonifera** (Michaux) Fosberg, comb. nov. *C. alba* var. *behnschi* Schelle, Handb. Laub. Benen. 366, 1903. *C. alba* var. *coloradense* Koehne, Mitt. Deutsche Dendr. Ges. (1903): 39, 1903. *C. alba* var. *elata* Koehne, Mitt. Deutsche Dendr. Ges. (1903): 39, 1903. *C. alba* var. *elongata* Koehne, Mitt. Deutsche Dendr. Ges. (1903): 39, 1903. *C. alba* var. *nitida* Koehne, Mitt. Deutsche Dendr. Ges. (1903): 39, 1903. *C. stolonifera* var. *flaviramea* Spaeth, Mitt. Deutsche Dendr. Ges. (1903): 39, 1903. *C. alba* var. *angustipetala* Wolf, Dendr. Gart. Kais. Forst. Pet. sep. p. 2, 1907. *C. alba* var. *splendens* Demcker, Mitt. Deutsch. Dendr. Ges. (1909): 326, 327, 1909. *C. stolonifera* var. *behnschi* Schneid., Ill. Handb. Laubh. **2**: 440, 1909. *C. stolonifera* var. *elata* Schneid., Ill. Handb. Laubh. **2**: 440, 1909. *C. stolonifera* var. *elongata* Schneid., Ill. Handb. Laubh. **2**: 440, 1909. *C. stolonifera* var. *nitida* Schneid., Ill. Handb. Laubh. **2**: 440, 1909. *C. stolonifera* var. *coloradense* (Koehne) Schneid., Ill. Handb. Laubh. **2**: 440, 1909. *C. alba* ssp. *stolonifera* Wangerin, in Engl. Pflanzenr. **41**: 53, 1910. *C. stolonifera* var. *angustipetala* Schneid., Ill. Handb. Laubh. **2**: 1041, 1912. *C. stolonifera riparia* Visher, Geogr. Geol. & Biol. So. Dak. 101, 1912. *C. stolonifera* var. *splendens* Schneid., Ill. Handb. Laubh. **2**: 1041, 1912. *Svida stolonifera* var. *flaviramea* Moldenke, Cult. Pl. 25, 1938.

Pubescence various, but with some hairs appressed and attached in middle; flowers with petals 2–3 mm. long; stone with smooth lateral faces.

This subspecies is found over the whole range of the species, but is less common at lower altitudes in the far West. It may be divided into the three forms treated below.

If the varietal category is used in place of subspecies the varietal epithet *coloradense* should be chosen from among several of the same date as it is the only one based on a wild plant. The rest are cultivated. It is only with reservations that I assign to this subspecies the various horticultural plants that have been given varietal names by Koehne and his contemporaries. Since the types, if they have been preserved, are now inaccessible, it is impossible to do more than place them as well as I can from the brief diagnoses given. This is an example of the difficulties besetting the botanist after even a slight amount of horticultural selection in a species. These plants are doubtless recognizable forms which should have horticultural names.

CORNUS SERICEA f. **stolonifera** (Michx.) Fosberg, comb. nov. *C. sericea* L., Mant. **2**: 199, 1771. *C. stolonifera* Michx. Fl. Bor. Am. **1**: 92, 1803. *C. purshii* G. Don, Gen. Syst. **3**: 199, 1834. *C. alba* var. *coloradense* Koehne, Mitt. Deutsch. Dendr. Ges. (1903): 39, 1903. *C. nelsoni* Rose, Contr. U. S. Nat. Herb. **8**: 54, 1903. *Svida* (or *Suida*) *stolonifera* Rydb. Bull. Torrey Club **31**: 572, 1904. *S. stolonifera* var. *riparia* Rydb. Bull. Torrey Club **31**: 573, 1904. *Cornus alba* ssp. *stolonifera* Wangerin, Pflanzenr. **41**: 53, 1910. *C. instolonea* Nels. Bot. Gaz. **53**: 224, 1912. *C. stolonifera riparia* Visher, Geogr. Geol. & Biol. S. Dak. 101, 1912. *Ossea instolonea* Nieuwl. & Lunell, Am. Midl. Nat. **4**: 487, 1916. *Svida instolonea* Rydb., Fl. Rocky Mts. 635, 1065, 1917.

Stems red to purple, rarely greenish or even yellow, glabrate or only thinly strigose; leaves with under surface strigose, sometimes with some spreading hairs near the midrib. Inflorescence strigose, flowers with petals 2–3 mm. long; stone slightly to conspicuously oblique, usually rather com-

pressed, usually smooth on the lateral faces, variable in size. Fruit white, rarely pale blue (MAINE: Dover, Piscataquis Co. *Fernald 305* [US]).

Found from Newfoundland, Keewatin, Mackenzie (Good Hope, 66° 15′ N., *Dutilly 8993* [LCU, USNA]), and Alaska (mainly near the south coast), south to New England, New York, Pennsylvania, Ohio, Indiana, Illinois, Missouri, and in the Rocky Mountains south to New Mexico, Chihuahua (*Townsend & Barber 26* [NY], *E. W. Nelson 4927* [US; TYPE of *C. nelsoni* Rose]), Arizona, and on the Pacific Coast to Southern California. Only a few eastern specimens, all from Pennsylvania (Reading, Berks Co., *Wilkens 6186* [PENN]; Haverford, Montgomery Co., *Schaeffer 1546* [PENN]; Wynnewood Sta., Montg. Co., *Walker 1932* [PENN]; from marsh at Centre Furnace, Centre Co., *Wahl 319* [PENN]) come from outside the glaciated area in the eastern portion of the range.

In the Rocky Mountains and westward it intergrades completely in all characters with ssp. *occidentalis*, often approaching the large flowers or sculptured stone, or both, of the latter. Perhaps the few eastern specimens with a somewhat ribbed stone may be the result of hybridization with *C. amomum*. Such is one from Tioga County, Pa. (*Wood 1586* [PENN, USNA]), which also has the brown pith of *C. amomum*. In the Great Lakes region, especially in sandy places it is largely but not completely replaced by f. *baileyi* and in the western central portion of the continent, from Nebraska to the Yukon region by f. *interior*.

CORNUS SERICEA f. **baileyi** (C. & E.) Fosberg, comb. nov. *C. baileyi* Coult. & Evans, Bot. Gaz. **25**: 37, 1896. *C. alba* ssp. *baileyi* Wangerin, in Engl. Pflanzenr. **41**: 55, 1910. *C. stolonifera* var. *baileyi* Drescher, Trans. Wis. Acad. **28**: 190, 1933. *Svida baileyi* Rydb., Brittonia **1**: 94, 1931.

Twigs purple, thinly appressed hairy or somewhat woolly when young, leaves thinly woolly beneath, some hairs attached at center, veins drying brownish beneath; inflorescence with at least peduncle spreading hairy, usually becoming more or less strigose distally, stone somewhat compressed, somewhat oblique, not ridged or furrowed except sometimes on edges.

Found in reasonably typical state in Michigan, Ontario, Minnesota, and northern Indiana, usually in sandy areas around the Great Lakes. One specimen, *Rothrock* in 1868 (Ph) from Centre County, Pennsylvania, has the leaf pubescence of this form but has no spreading hairs on the peduncle.

CORNUS SERICEA f. **interior** (Rydb.) Fosberg comb. nov. *Svida interior* Rydb., Bull. Torrey Club **31**: 572, 1904. *Cornus interior* Petersen, Fl. Nebraska 163, 1912. *Ossea interior* Lunell, Am. Midl. Nat. **5**: 239, 1918. *Cornus stolonifera* var. *interior* St. John, Fl. S. E. Wash. 303, 1937.

Stems purple, noticeably close-woolly when young, leaves strigose beneath, or rarely with spreading hairs especially near midrib, veins not especially prominent beneath, drying brownish; inflorescence spreading pubescent or woolly, at least on peduncle; stone oblique, somewhat compressed, variable in size.

A middle-western form, mostly collected in Nebraska, but extending east to Lorain County, Ohio (*Ricksecker* in 1895 [US]), west to Pikes Peak Forest Reserve, Colorado (*Flintham* [US]) and Cascade County, Montana (*Palmer 36943* [US]), (*Flint 22* [USFS]), north through the Dakotas, to Wood Buffalo Park, Mackenzie Basin, Canada (*Raup 2908* [US]), and to

the Yukon Valley.[1] One specimen is available from Matanuska, coastal Alaska (*Anderson 938* [US]).

CORNUS SERICEA ssp. **occidentalis** (T. & G.) Fosberg, comb. nov. *C. sericea* var. *occidentalis* T. & G., Fl. N. Am. **1**: 652, 1840.

Pubescence largely spreading, petals about 4 mm. long, stone very oblique, furrowed or roughened on lateral faces.

Pacific coast region from Canada to Southern California. Contains the following two forms. In the synonymy for this subspecific name, only the name-bringing synonym is given. Others may be found under the respective *formae*.

CORNUS SERICEA f. **occidentalis** (T. & G.) Fosberg, comb. nov. *C. sericea* var. *occidentalis* T. & G., Fl. N. Am. **1**: 652, 1840. *C. pubescens* Nutt., Sylva **3**: 54, 1849 (not Willd. in R. & S. Syst. Mant. III: 252. 1827). *C. occidentalis* Cov., Contr. U. S. Nat. Herb. **4**: 117, 1893. *Svida pubescens* Standl., Smiths. Misc. Coll. 56 (33): 3, 1912. *Cornus californica* var. *pubescens* Macbr., Contr. Gray Herb. **56**: 54, 1918.

Branchlets green to purple, thinly spreading pubescent, leaves variable in size, spreading pubescent beneath, often densely so, inflorescence conspicuously spreading pubescent, even on smaller divisions, stone as in f. *californica* but less often ridged, sometimes scarcely compressed.

Intergrades freely with f. *californica*.

Rare in coastal California Mountains (one specimen from San Bernardino Mountains) from San Diego County north, commoner northward, as far as British Columbia, east to Idaho.

CORNUS SERICEA f. **californica** (Mey.) Fosberg, comb. nov. *C. californica* C. A. Mey., Bull. Phys.-Math. Acad. Petersb. **3**: 373, 1845. *C. torreyi* Wats., Proc. Am. Acad. **15**: 145, 1876. *C. pubescens* var. *californica* Coult. & Evans, Bot. Gaz. **15**: 37, 1890. *Svida californica* Abrams, Bull. N. Y. Bot. Gard. **6**: 429, 1910. *S. torreyi* Heller, Cat. ed. 3: 273, 1914. *Cornus californica* var. *nevadensis* Jepson, Man. Calif. Fl. Pl. 733, 1925. *C. stolonifera* var. *californica* (Mey.) McMinn, Ill. Man. Calif. Shrubs. 377, 1939.

Branchlets greenish to red or purple, leaves ample, tending to be ovate, pubescence spreading beneath, inflorescence usually not very densely pubescent, with spreading hairs at least on the peduncle, appressed on smallest divisions, flowers relatively large, stone quite variable in size and shape, usually somewhat compressed, often quite broader than long, usually very oblique, generally more or less ridged or irregular longitudinally.

Common in California except the Great Valley floor, deserts, and alpine zone; extending north to British Columbia and Idaho, east to Nevada.

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[1] A series of collections made in northwestern Canada in 1940 by Dutilly may give a rough idea of the northern extension of this form. Alberta: Chipewyan, Athabaska L., 58° 45′ N., *Dutilly 8280*. British Columbia: Francois, 59° N., *Dutilly 8710*. Mackenzie: Fort Smith, Slave River, 60° N., *Dutilly 8117, 8118, 8153;* Fort Liard, 60° N., *Dutilly 8618;* Fort Simpson, Mackenzie River, 61° 50′ N., *Dutilly 8588;* Fort Norman, Mackenzie River, 64° 54′ N., *Dutilly 8838* [all LCU; some duplicates USNA].

BULLETIN OF THE TORREY BOTANICAL CLUB

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A NEW DUSSIA AND ORMOSIA AVILENSIS

JOHN H. PIERCE

The original description of *Ormosia avilensis* Pittier is bigeneric and in need of clarification. The foliage and fruit described are clearly those of *Ormosia*, while the flower is that of *Dussia*. The material collected or identified by Pittier is also bigeneric and there is further some question as to the number cited for the type specimen. The mixture of numbers, dates, and bigeneric material is so confusing that for the sake of clarity a discussion of each specimen involved is here presented.

Delgado 37, April 1937: cited by Pittier, presumably through typographical error, as the type of *O. avilensis* (in fruit); also as the type of *Pithecolobium pulchellum* Pittier (in flower). The flowering specimen so numbered is actually, in the opinion of the author, *Pithecolobium pulchellum* Pittier. No fruiting specimen of this number corresponding to the description of *O. avilensis* has been found.

Delgado 47, March 1937: identified by Pittier as *O. avilensis*, actually *Dussia coriacea* Pierce. Since Pittier cites a fruiting specimen as type of *O. avilensis* it is obvious that the original floral description was not taken from the type. This number was probably the basis for the original floral description.

Delgado 35, March 1937: both the foliage and fruit of this sheet fit the original description, if we exclude the floral description, and it is probably the actual type of *O. avilensis* Pittier.

Pittier 47, March 1937: this number consists of two sheets collected and identified by Pittier as *O. avilensis*. One sheet is *O. tovarensis* Pittier, the other consists of the foliage and fruit of *Dussia coriacea* Pierce and the seeds of *O. tovarensis* Pittier.

It seems probable that when Pittier described *O. avilensis* he had before him two or more of the specimens listed above and that he based the floral part of the description on *Delgado 47*, the rest on *Delgado 35*. This confusion can perhaps best be clarified by selecting as the LECTOTYPE of *O. avilensis Delgado 35*. The floral portion of the original description is excluded from *Ormosia* and refers to *Delgado 47*, which then becomes the TYPE of *Dussia coriacea* Pierce, described below.

O. AVILENSIS Pittier, Bol. Soc. Venez. Cien. Nat. **4**: 84. 1937. emend. Pierce (excluding the floral description). LECTOTYPE: *Delgado 35*, flowers unknown; Selvas del Avila, Venezuela.

Dussia coriacea Pierce, sp. nov. Arbor 20–25 m. alta; ramulis adultis puberulentibus; foliolis 5, oppositis, laminis lateralibus oblongo-ovatis, ter-

minalibus obovatis, 7–9 cm. longis et 3.5–6 cm. latis, basilaribus minoribus, supra glaberrimis, opacis, subtus uniforme rufo-tomentosis, venis lateralibus 10–14, prominentissimis, nervis transversalibus pluris, prominentissimis; floribus racemosis, ad apicem ramulorum novarum defoliatorum aggregatis; bracteolis ad basim calycis, obovatis acutis; calyce 5-lobo, subaequitanti; petalis lilacinis; vexillo suborbiculari, apice acutiusculo, extus plus minusve ferrugineo-pubescente; alis oblongo-lanceolatis, obliquis, minutissime pubescentibus; petalis carinalibus alis majoribus, valde inaequilateralibus, ovato-lanceolatis, infra ad suturam ferrugineo-pubescentibus; staminibus 10, ad basim leviter connatis; legumine maturo late fusiforme, fulvo-tomentoso; seminibus ignotis.

TYPE: *Delgado 47*, in flower, Selvas del Avila, Venezuela (Herb. N. Y. Bot. Gard.). The fruit characters taken from *Delgado 153* (at N. Y.).

This species is known only from the type locality and is readily distinguished from the other species of the genus by the small number of leaflets, the coriaceous texture and uniform pubescence of the leaflet and the smaller fruit. The pubescence suggests a relationship with *D. sanguinea* Kr. & Urb. while the fruit shape is close to *D. cuscatlanica* (Standl.) Standl. & Steyermark.

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BULLETIN OF THE TORREY BOTANICAL CLUB

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NUCLEAR BEHAVIOR IN THE MUCORALES—II. THE RHIZOPUS, PHYCOMYCES AND SPORODINIA PATTERNS

VICTOR M. CUTTER, JR.[1]

In a preceding paper (8) the nuclear behavior in eight species of the Mucorales was described, and the characteristic type of behavior designated as the *"Mucor"* pattern. The results of this comparative study indicated that in these species nuclear behavior followed the same basic scheme at corresponding stages in the life cycle. The predominant characteristics of this pattern were the presence of the haploid condition throughout the mycelial stages, karyogamy and reduction division occurring before the onset of the dormant period in the zygote; and the almost immediate resumption of the haploid condition before the accumulation of reserve products takes place in the zygote. Further features of this pattern were the rather short dormant period in the zygote, 1–5 months depending upon the species concerned, and the complete segregation of sex at the time of meiosis. Thus the diploid condition in this group of species was transitory, never persisting for more than a few days. In the present paper the nuclear behavior in six additional species will be discussed. In these species, *Rhizopus nigricans* Ehrenb., *Absidia glauca* Hagem., *Tieghemella coerulea* Naumov, *Phycomyces blakesleeanus* Burgeff, *Phycomyces microsporus* Van Tiegham, and *Sporodinia grandis* Link, the nuclear behavior falls into three different categories. The same techniques previously employed (8) were used in this study, and the species were studied comparatively at all stages in the life cycle. As in the preceding paper no attempt will be made to review extensively the literature on this subject since several adequate reviews are already extant, and stages in the life cycle which have already been adequately portrayed will not be reillustrated here. Reference to these previous investigations will be made in the appropriate places.

RHIZOPUS NIGRICANS Ehrenberg. This is undoubtedly the most frequently observed and familiar species in this order. It was with *Rhizopus nigricans* that Blakeslee initiated his brilliant investigations which led to the concept of heterothallism and homothallism in the lower fungi, and to the realization that the formation of zygospores in the Mucorales was fundamentally a sexual process. The early work on this problem has been admirably summarized by Blakeslee (2).

[1] Publication of the figures in this and the previous paper by Dr. Cutter was made possible by the Lucien M. Underwood Memorial Fund. Pages in excess of the usual number were printed at the expense of the author.

The details of nuclear behavior and sporangium formation in the asexual phase of this fungus were very accurately described by Swingle (25) and his description confirmed by Moreau (20). The results of the present study as far as the asexual stages are concerned, are in complete agreement with those of Swingle and Moreau, and no further attention will be devoted to them here.

Cytological investigations on the nuclear behavior in the sexual phase have been carried out by Namyslowski (21), Macormick (19), Moreau (20), and Baird (1). Namyslowski reports the presence of numerous nuclei in the young zygospore, but has not succeeded in distinguishing any nuclear fusion. Macormick, in a preliminary note on her research, reports that numerous nuclei enter the young coenozygote, and there increase in size. Thereupon, all the nuclei except two disintegrate, and these remain embedded in a coenocentrum. This coenocentrum persists until quite late in the development of the zygospore but in mature zygospores there are many nuclei of the same size as those in the mycelium. She is unable to interpret this condition nor does she indicate her conception of a mature zygospore. Moreau does not confirm Macormick's observations and feels that the nuclear behavior in *Rhizopus* differs in no fundamental way from the other members of the Mucoraceae which he has studied. He figures multiple nuclear fusions accompanied by the degeneration of unfused nuclei. He does not follow the ultimate fate of the fusion nuclei, but it is clear that he believes the meiotic process to occur at the time of zygospore germination.

Baird concerns himself more with the behavior of the individual nucleus in *Rhizopus* and the changes which it undergoes during the life cycle than with an investigation of the changes and relationships of the entire nuclear complement. He states that the nuclear behavior in *Rhizopus* is essentially the same as that described by him in *Phycomyces*. In neither of these forms has he been able to discern nuclear fusions at any stage. None of these authors has studied the nuclear condition in the germinating zygospores. This germination process has been reported only by Blakeslee (3) who observed it twice.

Callen (7), working with a recently described homothallic species, has traced the nuclear behavior through the development of the zygospore but he was unable to obtain germination of these spores. In this species, *Rhizopus sexualis* (Smith) Callen, the nuclei associate in pairs during the formation of the coenozygote but he feels that it is doubtful whether any nuclear fusion occurs. Nuclear degeneration also takes place at this stage but ceases as the zygote matures. The nuclei remain in the paired condition as the zygote becomes dormant. Callen's account of nuclear behavior in *R. sexualis* is quite reminiscent of the nuclear cycle described below for two species of *Phycomyces*, and perhaps will prove to be an intermediate form between the *Rhizopus* and *Phycomyces* patterns.

The most striking difference between the nuclear condition in the progametangia and young coenozygote of *Rhizopus* and that seen in the species studied previously is the vast number of nuclei present per given unit of cytoplasm. These nuclei are rather large and appear proportionately far more numerous than in the corresponding stages of other species. Mitotic divisions in this species present the same general aspect as those described elsewhere (8). Centrosomes are rather regularly present, and the achromatic spindle is fairly well developed. No discrete chromosomes have been distinguished in any of the division stages yet encountered.

The young progametangia develop slowly and the suspensors are usually not delimited until the second day after contact has been established between the zygosporic hyphae (fig. 4). The wall separating the suspensors from the gametangia is formed by a cleavage furrow which arises at the periphery of the progametangial cell and progresses towards the interior (fig. 5). Both Moreau and Macormick have stated that a difference in the staining reaction of the two gametangia can be demonstrated, even after the formation of the coenozygote. If this is true, it is a point of great significance, since it would constitute good evidence of a physiological differentiation between the plasmas of the two opposed strains. These observations are not substantiated in the present study, and any differential staining reaction of the cytoplasm of the gametangia appears purely coincidental.

Development of the coenozygote is slower than in the species previously observed. During this period mitotic nuclear divisions occur with great rapidity and tremendous numbers of unfused, expanded nuclei are present in the coenozygote as the exospore is formed. At this stage karyogamy occurs between many of the nuclei present in the cell, but a large number of the supernumerary nuclei do not engage in fusion and remain for some time in the unfused condition. Karyogamy differs somewhat from that described in *Mucor genevensis* and *Blakeslea trispora* (8) in that the paired nuclei do not enlarge greatly before fusion, nor do these nuclei remain associated in pairs for any length of time before fusion occurs. The fusion or diploid nuclei can be distinguished readily from the unfused nuclei by their greater size and more prominent reticulum and central body (fig. 7). In the suspensors the nuclei are very prominent at this stage, but shortly assume the unexpanded phase, and ultimately degenerate.

Both fused and unfused nuclei remain in evidence for several days until the endospore has been deposited. As this endospore is developed the unfused nuclei begin to degenerate, and before the dormant condition is reached all the unfused nuclei have apparently disintegrated. This degeneration is initiated in some cases at least by well marked amitotic divisions which are frequent during this period. Zygospores ten days old have become, to all appearances, dormant.

The oil plastids are not particularly prominent in *Rhizopus*, but can occasionally be demonstrated. On the other hand, mucorine crystals are extremely abundant and are quite frequently aggregated into groups. These groups of crystalline structures may be synonymous with the structures which Macormick identifies as coenocentra. Aside from this no evidence of coenocentra have been observed. There is a considerable amount of oil present in the vacuoles which arises in the cytoplasm as nuclear degeneration commences. It seems likely that the degeneration of these unfused nuclei may augment this supply of oil, if not accounting for all of it.

During the dormant period the fused nuclei assume the unexpanded state but are still conspicuously larger than the nuclei present in mycelia and gametangia (fig. 8). The oil reserve of the dormant zygospores is largely confined to the central vacuoles which have arisen by the confluence of many smaller ones. The cytoplasm becomes restricted to a thin peripheral layer and the mucorine crystals largely disappear. The exospore and endospore of the dormant zygotes is extremely thick; *Rhizopus* is by far the heaviest-walled species yet observed in the Mucorales. The dormant period persists for approximately a year, during which no visible change occurs in the spore contents.

The difficulty of germinating the zygospores of *Rhizopus* has become almost proverbial among mycologists who have worked with this species. Blakeslee succeeded in inducing zygospores to germinate only twice, in both cases after a rest period of more than a year. These germinations, however, did not result in the production of normal sporangiophores and spores. During the course of this study a number of zygospores of this species have been germinated, but germinations have never proceeded normally. Whenever germinations were obtained only abortive germ tubes were produced, and neither sporangia nor mycelia were developed by these tubes. Further remarks upon this subject will be presented in a subsequent publication.

The nuclear condition observed during germination differs markedly from that described in *Mucor genevensis* (8). At the onset of renewed activity in the cytoplasm, 2–3 days before germination, the cytoplasm, which has been restricted to a thin layer adhering to the endospore wall, begins to increase in extent and becomes vacuolate, with the oil reserve, previously restricted to the central vacuoles, now becoming dispersed throughout the cell. This oil interferes with precise staining of the nuclei at this period, but nuclear division apparently takes place rapidly, for as the oil disappears many small expanded nuclei can be discerned, arranged in the peripheral regions of the spore. There are still a few fusion nuclei present at this stage but they all disappear before the formation of the germ tube. The smaller nuclei are several times more numerous than were the fusion nuclei during the dormant period. These unfused nuclei undergo mitotic divisions as the

germ tube develops. The heavy zygospore walls of *Rhizopus* do not rupture as widely as in other species where this process has been observed, and the germ tube gains access to the exterior through a rather restricted pore (fig. 9). This germ tube grows slowly and a few mitotic divisions can be seen in the developing tube. At the end of several days' growth, at which time the tube may have reached a length of 1 centimeter, it slowly shrivels and cytoplasmic activity ceases, even when the tube is in contact with nutrient media. It appears from the results outlined above, that the reduction process must occur in the first divisions of the fusion nuclei as renewed growth of the cytoplasm takes place in the germinating spore, since the nuclei, after these first few divisions, are notably smaller than those present in the dormant zygospore. However, no other indications have, as yet, been seen which were suggestive of meiotic divisions, possibly because of the difficulties in distinguishing nuclei in the oil soaked cytoplasm of the early germination stages. If this interpretation is correct, *Rhizopus* shows a somewhat advanced condition over those species described under the "*Mucor*" pattern, where the diploid condition is present for a few days at most; and where reduction division presumably occurs before the dormant condition is reached. In *Rhizopus* the diploid condition seems to be prolonged until the onset of germination.

Absidia glauca Hagem. This heterothallic species has been investigated cytologically only by Ling Young (18) although Moreau (20) has studied *Absidia orchidis* which is very closely related to and perhaps synonymous with it. Both these authors agree that in the younger stages the nuclei are very minute and appear even more numerous than is usually the case in the Mucorales. Moreau describes prominent fusion nuclei which appear after the formation of the coenozygote, and he states that many supernumerary nuclei disintegrate. Ling Young corroborates Moreau in this. The older stages of the zygospore and the germination stages have not yet been described, as far as the author is aware. Moreau investigated the asexual reproduction stages and noted that the sporangiospores were uninucleate. He describes the process of spore formation as similar to that described by him for *Mucor spinescens* (20).

As far as could be determined in this study, the development of the sporangiophore and sporangium, and sporangiospore formation differed in no way from that previously described for *Absidia spinosa* (8). The nuclei are somewhat smaller and proportionately more numerous than in the latter species. The progametangia develop in the usual way and are supplied with very numerous expanded nuclei. The suspensor appendages develop as in *A. spinosa*, but in this species are produced in about equal numbers on both suspensors, and are not confined to the larger suspensor as previously re-

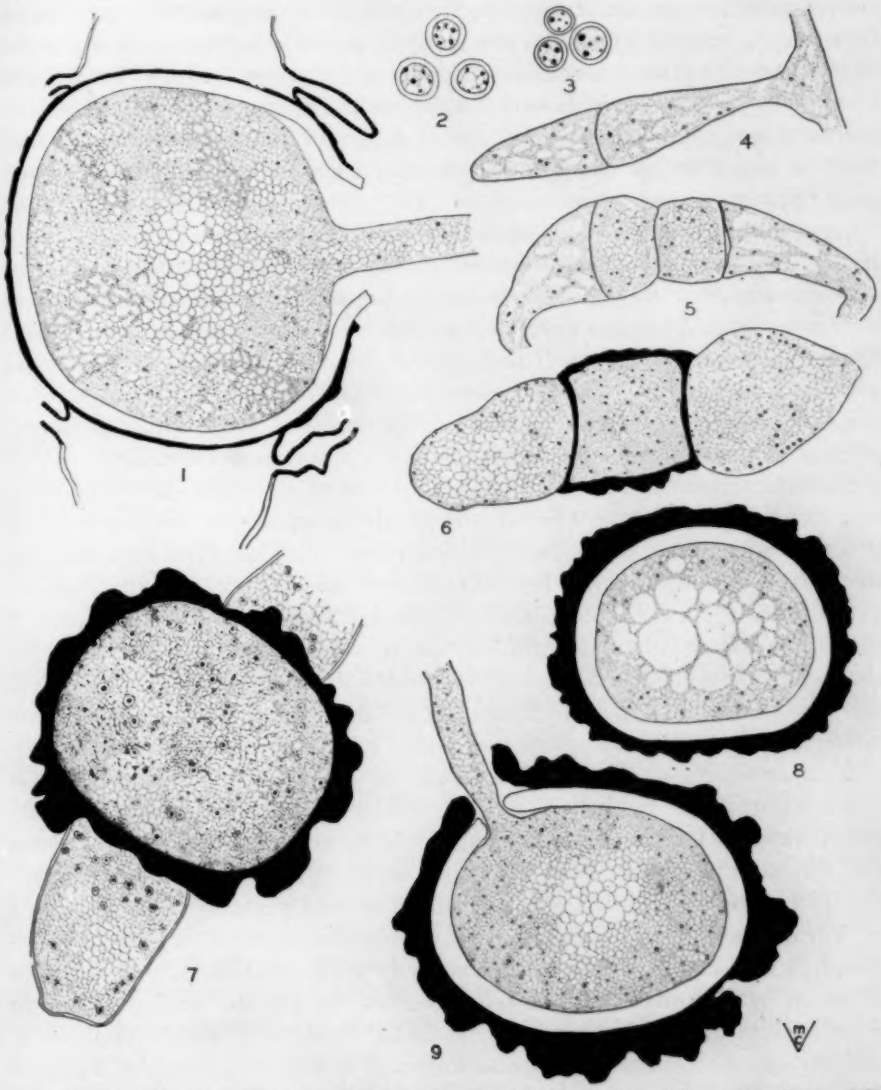

FIG. 1. *P. blakesleeanus*, germinating zygospore (Flemming's; Haematoxylin). ×170. FIG. 2. *P. blakesleeanus*. Sporangiospores from asexual sporangium; unfused unexpanded nuclei (F.A.A.; Buffer). ×960. FIG. 3. Sporangiospores from germ sporangium. Fused and unfused unexpanded nuclei (F.A.A.; Buffer). ×960. FIG. 4. *Rhizopus nigricans*, progametangia 7 hours old (Flemming's; Haematoxylin). ×400. FIG. 5. Gametangia 24 hours old (Flemming's; Haematoxylin). ×400. FIG. 6. Zygospore 36 hours old, unfused expanded nuclei (Craf; Cahal-Brozek). ×400. FIG. 7. Zygospore 3 days old, fused and unfused nuclei. Note prominent unfused nuclei in suspensors (Flemming's; Triple). ×400. FIG. 8. Dormant zygospore, fused unexpanded nuclei (Gilson's; Feulgen). ×400. FIG. 9. Germinating zygospore 13 months old, fused and unfused nuclei expanded (Flemming's: Triple). ×400.

ported in *A. spinosa*. In *A. orchidis* Lendner (17) has illustrated copulation between the young appendages produced from the two suspensors of a zygospore, thus forming a secondary zygospore upon appendages which here functioned as zygosporic or sexual mycelium. The same situation has been observed several times in our cultures of *A. glauca* and indicates clearly that there is a localization of oppositely sexed plasma in the suspensors as well as in the gametangia.

As in *Rhizopus nigricans*, nuclear divisions continue with great rapidity in the developing coenozygote and karyogamies are not in evidence until the exospore has been formed. The fusion nuclei are large and prominent, but they are of the *Rhizopus* type rather than of the type encountered in the species showing the "*Mucor*" pattern. All the nuclei present in the young zygospore do not fuse, and for several days after karyogamy has occurred, the degeneration of unfused nuclei may be observed. Apparently all supernumerary nuclei degenerate before the zygospore becomes dormant.

In the dormant zygospore, because of the great abundance of oil plastids, it is difficult to ascertain whether all the nuclei remain in the fused condition, but no evidence of nuclear division of any sort has been seen between the time when the zygospore becomes dormant and the onset of germination. Presumably the nuclear condition during the dormant period is similar to that in *Rhizopus* where the diploid unexpanded phase persists until the spore germinates. Germination in our material occurred between the sixth and seventh month after the formation of the zygospore. The nuclear condition in the germinating spores is identical with that described in *Rhizopus*, and apparently meiosis takes place during the first few divisions of the nuclei before the germ tube is formed. The germ tube develops into a long stolon which bears a fasicle of sporangia in the same manner as the vegetative mycelium. The sex of all the spores in any germ sporangium is either plus or minus. Segregation of sex is thus apparently complete at meiosis.

The similarity of nuclear behavior in *Absidia glauca* with that in corresponding stages of *Rhizopus nigricans* leads to the conclusion that the relationships of the genus *Tieghemella*, erected by Berlese and de Toni to accommodate the species previously included in *Absidia* which resemble *A. orchidis* and *A. glauca*, are closer to *Rhizopus* than they are to the *Hagemia* section of *Mucor* and the *Absidia spinosa* type. In this material it is not possible to corroborate Moreau's conception (20) that *A. glauca* shows essentially the same cytological behavior as *A. spinosa*.

TIEGHEMELLA COERULEA (Bainier) Naumov. This is another heterothallic species segregated from *Absidia* by Naumov. It is distinguished from *Absidia glauca* only by minor differences in mycelium color and spore size. It has not been previously investigated cytologically. In the strain used in

the present study the young mycelia of the plus strain is pure white in color and the young mycelia of the minus strain cerulean blue. This constant color difference between the sexes renders this material particularly favorable for studies concerning sexual segregation, and investigations are being carried out along this line.

From a study of a large number of zygospores it appears that in this species the appendages are developed on both suspensors less frequently than in *A. glauca*. In this respect the species may be intermediate between *A. spinosa* and the forms in the genus *Tieghemella*. As far as can be determined the nuclear behavior differs in no way from that already described in *A. glauca* and, therefore, is obviously different from that in *A. spinosa*.

PHYCOMYCES BLAKESLEEANUS Burgeff. The genus *Phycomyces* has been very thoroughly investigated by many workers. Blakeslee (2) first demonstrated heterothallism in *P. nitens* and tested the sexual condition of the sporangiospores produced in the germ sporangia. His work has been confirmed by Burgeff (4) and others. Burgeff (6) has discussed the taxonomy of the species used in the present investigation and indicates that the laboratory strain of this fungus which had been widely distributed as *Phycomyces nitens* Kunze represents in reality an undescribed species named by him *P. blakesleeanus*. *P. nitens* Kunze is a rare and obscure species, and has probably never been investigated cytologically. All these workers agree that in the germ sporangium of *P. blakesleeanus* segregation of sex is not complete, and sporangiospores of plus, minus, and homothallic or bisexual potentialities are produced. Burgeff (5) in a very extensive study of this species and its various mutants, has advanced the hypothesis that the heterocaryotic nature of some of these sporangiospores is due to a partial diploid condition, resulting from only a partial reduction of the fusion nuclei in the zygospore. Krafcyzk (15) in observations upon a similar phenomenon in *Pilobolus crystallinus*, has substantiated this theory. Burgeff (5) has also presented a brief description of the nuclear behavior throughout the life cycle. He finds that in all the early zygote stages many unfused nuclei are present; these persist in an apparently unfused condition throughout the development of the zygospore and during the dormant period. He has not been able to demonstrate a nuclear membrane on these nuclei and describes them as consisting merely of a single homogeneous chromatin body without any "nucleolus." No fusions are noted until the time of germination, when the nuclei in the peripheral regions of the spore arrange themselves in pairs and fuse. These fusion nuclei are characterized by the presence of a nuclear membrane and a "nucleolus" and are larger than the unfused or haploid nuclei. He states that the diploid nuclei always have a membrane and

nucleolus, and that he uses this character to distinguish them from the haploid nuclei.

As the germ tube develops and forms the germ sporangium fundament "mitotic" divisions occur. Burgeff states that this mitotic process is very difficult to follow. He has observed prophases in which the nucleolus disappears, and later stages in which there are 24 chromosomes which have been derived from the single chromatin body of the nucleus. He finds that the division figures are intranuclear, and that 12 chromosomes move to each pole, where they assume a new membrane. He did not observe metaphases. These mitoses are interpreted as the heterotypic division, and are followed by a homeotypic division in which distinct chromosomes are again visible. Successive divisions then occur which give rise to a large number of nuclei which lack membranes. There are now present in the sporangial fundament nuclei with and without membranes, as well as presumably unreduced diploid nuclei. Theoretically spores which receive these unreduced nuclei give rise to heterocaryotic mycelium. Spore formation in the germ sporangium, according to Burgeff's description, differs from the condition reported by Swingle (25) in the vegetative sporangia. Burgeff finds only a single nucleus entering each spore initial which then becomes multinucleate by continued nuclear divisions, whereas Swingle reports that the spore initials are multinucleate from the time they are delimited by vacuoles, and he has been unable to observe any nuclear divisions within the spore initials. Burgeff has not illustrated any of the nuclear stages, and the only stain which he has employed is iron alum–haematoxylin, which is notoriously inefficient when much reserve material is present.

Moreau (20) has carried out cytological studies on the formation of the sporangia in *Phycomyces nitens*, where his results are in accord with those of Swingle (25), and upon the early stages of the zygospore where he reports nuclear fusions occurring at the stage where the exospore is deposited. These fusion nuclei are small and hard to distinguish from the unfused nuclei. Their ultimate behavior has not been determined. Keene (14) has investigated the nuclear condition in the zygospores of the same species up to 6 months of age but has not observed germination. She reports that in the young coenozygote the nuclei associate into groups of 12–16, after which a fusion of the nuclei in pairs results in a decrease in the number of nuclei and a slight increase in the size of the fusion nucleus. She finds that in zygospores six months old nuclei of the "typical" form are present in much reduced numbers in the thin parietal layer of cytoplasm in the dormant zygospore. Her illustrations of the early stages are very accurate, and for that reason these stages will not be reillustrated here.

Baird (1) has studied the nature of the nucleus of *P. nitens* and the changes it undergoes throughout the life cycle. He finds no nuclear fusions

at any stage and can discern no evidence of nuclear divisions in the zygospore or germ tubes. He notes, however, the grouping of the nuclei in the formative stages of the coenozygote, previously mentioned by Keene. He also describes the process of vacuole formation, and indicates that the vacuoles arise within the nuclei; furthermore, he believes these vacuoles function in nuclear division. His account is confusing and seems based upon insufficient evidence. Ling Young (18) has also noted the presence of grouped nuclei in the early zygospore stages, and he reports fusions occurring after this stage. The unfused nuclei then degenerate, and function in the nourishment of the fusion nuclei. He does not investigate the further development of the zygospore.

Most accounts of the development of the progametangia and young coenozygote of this species are in agreement. These organs are multinucleate, mitotic divisions are in evidence as they increase in size, and the nuclei are extremely numerous. The development of the suspensor appendages is the same as that already described in *Absidia*, save that in *Phycomyces* they are branched. The individual nucleus in *Phycomyces* is very small when compared with such species as *Mucor genevensis* and *Blakeslea trispora*, rarely measuring more than two microns in diameter, in the unfused condition. Only Burgeff has been unable to demonstrate a nuclear membrane on the unfused nuclei at these early stages. His use of Juel's fixative may account for the discrepancy since this reagent, which contains a high percentage of alcohol, has proved quite unsatisfactory for the precise fixation of these small nuclei. As the last remnants of the wall which separates the gametangia are absorbed, the nuclei in the coenozygote come together into very characteristic groups. The nuclei are still expanded and these large nuclear groups might, in improperly fixed material, be mistaken for fusion nuclei. As far as can be determined, no karyogamy takes place at this or the immediately succeeding stages. At this time mucorine crystals become very abundant in the cell and even in the suspensors. Shortly afterwards, oil plastids are distinguished, although these do not become as prominent as in *Absidia spinosa* and *Mucor genevensis*. Keene, Moreau, and Ling Young have all reported nuclear fusions occurring soon after the nuclei associate in groups, but they all indicate that this fusion does not involve all the nuclei in the cell and that the unfused nuclei degenerate. In the present material no indication of either nuclear divisions, fusions, or degenerations can be distinguished after the nuclei have become aggregated into groups. To all appearances the nuclear condition in the zygospore remains unchanged until the onset of dormancy. As the zygospores enter the resting period after the endospore has been deposited, the only change visible in the nuclear condition is the apparent loss of the nuclear membranes. This is usual in all species at this stage when the nuclei change from the expanded to the unexpanded stage

coincident with a decrease in cytoplasmic activity (8). The grouped arrangement of the nuclei seems to be retained throughout the dormant period, which in this species persists for approximately six months. Blakeslee (2), Orban (22), and Burgeff (4) have discussed the duration of the dormant period, and the time during which the zygospores remain viable. From their observations and the results of the present investigation, it seems safe to conclude that the zygospores are capable of germinating at any time between the sixth and thirteenth month after their formation. Zygospores ready to germinate may be recognized externally by the mottled or translucent appearance of the exospore wall.

In the period just preceding the germination of the zygospores very clearly defined nuclear fusions occur. These do not, however, involve all the nuclei present in the cell. Estimating the proportion of nuclei which undergo karyogamy at this stage is a somewhat doubtful procedure, but possibly half the nuclei become enlarged to the extent where it seems reasonable to assume that they represent diploid nuclei. The fusion is of the *Rhizopus* type and the nuclei do not enlarge greatly before fusion. The grouped arrangement of the nuclei noticeable during the preceding stages of zygospore development is now lost and the fused and unfused nuclei are scattered without regularity in the peripheral regions of the cell. The central region previously occupied by several large vacuoles becomes alveolate, but remains sterile as far as the nuclei are concerned. One or two days after fusion has occurred the zygospore walls are ruptured and a thick germ tube is pushed out (fig. 1). During the early stages of tube formation mitotic divisions of both the fused and unfused nuclei are in evidence, and both types of nuclei are present in the growing tube and in the fundament of the germ sporangium. It appears probable that the meiotic divisions in at least a portion of the diploid nuclei occur at this stage as Burgeff has indicated, but as yet characteristic division stages which might be interpreted as meiosis have not been observed in this material. All observations made upon spore formation in the germ sporangia indicate that these structures are formed in exactly the same manner which Swingle (25) has described for the asexual sporangia. The spore initials are, except in an occasional instance, multinucleate from their inception, and Burgeff's statement that they are at first uninucleate cannot be substantiated. Nuclei of two sizes are certainly present in a portion of the spores of the germ sporangium (fig. 3), but there is no regularity whatever in this feature. It is presumed that both fused and unfused nuclei are distributed by chance in the spore initials, the ultimate distribution of the two types of nuclei probably forming the basis for the sexual character of the ensuing spores and mycelium. No indications have been found of nuclear division of any type within the spore initials or the maturing spores. If part of the diploid nuclei present in the germinating zygospore have undergone

meiosis in the germ tube or the fundament of the germ sporangium, then it becomes apparent that nuclei of three types must be incorporated in the spores of this sporangium; unfused nuclei which have persisted throughout the development of the zygospore, unreduced fusion nuclei, and nuclei which have undergone reduction division. The sexual character of the mycelium resulting from the germination of these spores is then determined by the balance existing between the potentially different nuclei present in them.

Spores which contain a predominance of unreduced or diploid nuclei, or a perfect balance of plus and minus nuclei presumably produce upon germination a potentially homothallic mycelium in which further sexual segregation occurs at a later date. Mycelium arising from spores which contain a majority of unreduced or haploid nuclei is influenced in its sexual behavior by the balance existing between nuclei of the opposite sexes. This condition will, of course, give rise to mycelia in which all intergradations of sexual potency, from strongly unisexual to strongly bisexual, can occur. The work of Blakeslee (2), Burgeff (5), and Krafcyzk (15) indicates that such sexual intergradation does occur in Mucors which show this incomplete segregation. It must be emphasized, however, that to date the only available cytological evidence that confirms such an hypothesis, is Burgeff's report of partial reduction of fused nuclei in the germ tube and young germ sporangium, and the present results which indicate that nuclei of two types, fused and unfused, are present in the spores of the germ sporangium. Further investigation of these critical stages is necessary in order to completely clarify the nature of the meiotic process.

In the hope of tracing the ultimate behavior of the unreduced nuclei which enter some of the spores of the germ sporangium, a great number of single-spore cultures of these spores were made. Some of these resulted in homothallic mycelia characterized by the production of pseudophores and homothallic zygospores as described by Blakeslee (2) and Burgeff (4). Homothallism of this type is, of course, phenotypic, as contrasted with the genotypic homothallism present in such genera as *Zygorhynchus* and *Sporodinia*. Development of the homothallic mycelia and zygospores of the F_1 generation as far as nuclear behavior was concerned apparently followed the same course described for the heterothallic cultures. Segregation of sex in the germ sporangium was again only partial, plus, minus, and neutral or homothallic mycelia again being obtained in the F_2 generation. The homothallic mycelia of this third generation was so weak in these cultures that no perfect zygospores were developed. It was therefore impossible to continue the study of homothallic segregation beyond the third generation. It would be expected from the fact that two types of nuclei were present in the germ spores of the first generation that these two types of nuclei would be in evidence in some of the early stages of the F_1 homothallic mycelia, but

in spite of particular efforts, no evidence of a heterocaryotic condition could be found in either the second or third generation except at the fusion stages in the zygospore of the germ tube and young germ sporangium and in the spores resulting from this germ sporangium. It is possible that the diploid nuclei present in these spores are reduced in the first few divisions after the spores germinate, and that second generation homothallism results from a perfect balance between plus and minus nuclei, rather than from a retention of the diploid condition, in some isolates. It is, of course, also conceivable that these diploid nuclei may degenerate in the early mycelial stages. As yet no technique for the adequate examination of these early mycelial stages of the homothallic segregants has been developed, since it is as yet impossible to determine the sexual character of any isolate until the reproductive organs are formed.

Observations on the asexual sporangia of heterothallic and homothallic isolates indicate that development proceeds in complete accordance with Swingle's (25) description; hence no further attention will be given to this phase of the life cycle.

PHYCOMYCES MICROSPORUS Van Tieghem. Material of this species was collected in North Carolina by G. A. Christenberry, who kindly contributed cultures for study. The fungus is smaller in all its dimensions than *P. blakesleeanus* but differs from the latter in no other important respects. It has not been previously investigated cytologically. No differences were observed between the nuclear condition in this species and in *P. blakesleeanus*, and the behavior of the spores in the germ sporangia were identical in their sexual expression. The zygospores germinate in 3–4 months, which indicates a somewhat shorter dormant period than in the aforementioned species.

SPORODINIA GRANDIS Link. Dangeard and Leger (10) were the first to investigate the nuclear condition in *Sporodinia*. They describe the young zygospore as containing many nuclei in a dense protoplasm; at a somewhat later stage nuclei of two sizes appear, and nuclei remain evident in the older stages of the zygospore as oil begins to accumulate. Leger continued this work independently (16) and described a number of anomalous bodies not observed by other workers. According to Harper (12), Lendner (17), and Ramsbottom (23), Leger's results must be questioned since they were obtained only by gross dissection with needles, and in crushed mounts, and these methods are obviously unsatisfactory for such minute structures. Dangeard (9), after a study of the nuclear condition in *Mucor fragilis*, returned to *Sporodinia*, and in light of the nuclear condition in *Mucor* he claimed a similar condition existed in *Sporodinia*, with the exception that the nuclei were very much more numerous. According to this interpretation,

nuclear fusions occurred in the maturing zygospore, and there were present in the older spores certain masses of mucorine crystals which resembled coenocentra. Moreau (20) has corroborated, in its essentials, the work of Dangeard.

Gruber (11) found numerous nuclei present in the early stages of the zygospore, and stated that there was a brief period of nuclear zonation in the young zygote, similar to that noted in many Peronosporaceae, the nuclei being more numerous in the parietal layer during this period. He found no disorganization of nuclei and no nuclear fusion, although he assumed that the latter took place at some stage in the life cycle.

Lendner (17) investigated the formation of the zygospores up to the point where the endospore is laid down. His account of the early stages agrees with those of other workers. However, he finds two large nuclei present in the newly formed zygospore, in addition to a great number of small nuclei lying scattered throughout the cell. These small nuclei divide and seem to be more numerous near the walls of the spore where they may function in the formation of the zygospore membrane. The two large nuclei fuse and occupy the exact center of the spore. He does not determine the fate of this fusion nucleus. Ramsbottom (23) has presented a very complete summary of the work on *Sporodinia* up to this point.

In 1914 Keene (13) published the results of an extensive study of the nuclear behavior in this species. She reports progressive nuclear fusions occurring as the protoplasm of the gametangia mingles, and as a result two types of nuclei are present in the young zygospore. The larger of these represent fusion nuclei. The unfused nuclei ultimately degenerate. She examined zygospores up to one year of age and in the older stages describes the formation of oil plastids which she likens to the elaioplasts of higher plants. In the mature zygospores, from 3 to 12 months old, there are numerous fusion nuclei present in the thin parietal cytoplasm which surrounds the large central vacuole. She states that this condition persists until germination, although she did not obtain germination. Mucorine crystals are reported in all the earlier stages.

Ling Young (18) has added a few points of interest to the accounts of other investigators on *Sporodinia*. He notes a tendency for the nuclei of the progametangia to aggregate into groups near the membrane which separates the gametangia. Fusions presumably take place during the formation of the young zygospore, but he states that it is difficult to distinguish the fusion nuclei, which are only slightly larger and more dense than the ordinary vegetative nuclei. He does not trace the ultimate behavior of the nuclei in the maturing spore. In azygospores of *Sporodinia*, where no fusion of protoplasts has taken place, there are numerous mitotic divisions as the spore develops and the nuclei aggregate into groups. It is difficult to ascertain

whether they fuse, but in the older spores there is a decreased number of nuclei and some difference in nuclear size. He does not feel that there is any fundamental difference between the nuclear behavior in zygospores and azygospores. Harper (12) has described the process of sporangiospore formation in the asexual sporangia of this genus. He finds that the protoplasm of the sporangial fundament segments into multinucleate portions which at maturity assume a wall and function as spores.

The early stages in the development of the thallus and azygospores have been very accurately worked out by Keene (13) and no further discussion of them is necessary. During nuclear division an achromatic spindle is developed, but it is very faint and centrioles can only occasionally be distinguished at the poles (fig. 19). At the tips of developing hyphae, sporangiophores, and zygophores threadlike mitochondria can be demonstrated by the use of basic fixatives (fig. 16). These appear closely similar to those already described in *Mucor genevensis* (8).

Mitotic nuclear divisions occur repeatedly during the development of the progametangia. As they reach their maximum size a darker staining area appears in the cytoplasm around the point of contact of these progametangia, extending some distance back into them (fig. 10). This presumably results from the diffusion of some enzymatic substance which causes the dissolution of the membrane separating the progametangia. It disappears shortly after the membrane has broken down (fig. 12). At this point Keene has described nuclear fusions which result in the presence of nuclei of two sizes, although she points out that the minute size of the nuclei make it difficult to determine whether there are true fusions or only divisions. The results of the present study show no evidence of any fusions occurring at this stage. No significant difference in nuclear size was seen which could not be accounted for on the assumption that certain of the nuclei have commenced to degenerate and hence are in the unexpanded phase. Mucorine crystals are sometimes very abundant and in other cases almost lacking. These crystals may at times be confused with the achromatic spindles of dividing nuclei in material stained in haematoxylin, but show no reaction to the Feulgen test and can thus be distinguished easily. Although many hundreds of spores have been examined no indication of the large fusion nucleus reported by Lendner has been seen. Figure 12 shows a young coenozygote just after the membrane which separated the progametangia has been absorbed. At the center of the spore the dark portion, which actually represents the remnants of this membrane with several included mucorine crystals, might, in material stained with Safranin such as Lendner used, he interpreted as a fusion nucleus. This figure corresponds well with his illustration of this fusion nucleus, and perhaps explains his interpretation.

Shortly after the formation of the young zygospore, the cytoplasm be-

comes denser, and through repeated mitotic divisions, the nuclei become much more abundant. At the same time the exospore is laid down. Keene has attributed the darkening of the cytoplasm to the presence of disorganizing nuclei, but in my preparations the nuclei do not appear to degenerate until a much later stage. In material fixed with basic fluids and stained in haematoxylin mitochondria are very numerous and group around the boundaries of the developing vacuoles, where they form a very characteristic reticulum, in the interstices of which the nuclei are suspended. Shortly thereafter oil accumulates in these vacuoles and the mitochondria begin to disappear. This would suggest that these structures function in the secretion of oil, a fact borne out by the researches of Tarwidowa (26) who described fat droplets as arising from the chondriome in *Basidiobolus ranarum*. Several authors have described a zonation of the nuclei in the zygospore at this time, and Keene suggests that the unfused nuclei gather near the periphery of the spore and there disintegrate. In material which had been thoroughly penetrated by the fixing fluids, no zonation of nuclei was ever encountered in this study, but when fixation had been too rapid and good penetration had not been secured, the nuclei frequently had a zoned aspect in the zygospore. Inasmuch as the nuclei near the periphery had in these cases been adequately preserved, their structure was apparent and they could be seen to be unfused, whereas those nuclei near the center of the spore were very poorly preserved and their size could not be definitely determined. Thus a fixation "artifact" may have been responsible for the description of a zonation stage in the zygospore.

About five days after the formation of the exospore, the heavy hyaline endospore begins to appear and in zygospores one week old the endospore is almost invariably present. By this time the reserve substances have become abundant and are accumulated in one or more large vacuoles in the center of the spore, while the cytoplasm is restricted to a thick parietal layer. As the cytoplasm becomes contracted and its activity ceases, the nuclei change to the unexpanded state. It seems probable that here a certain amount of nuclear degeneration occurs, since in the restricted cytoplasm the nuclei appear no more numerous than they do in the younger stages (fig. 14). A few amitotic divisions have been observed at this stage which tends to bear out the contention (8) that amitosis may be the first indication of nuclear degeneration. The large oil plastids have arisen by the coalescence of many smaller ones in the manner described by Keene (13). No further changes take place in the spore until germination ensues.

Blakeslee (2) has reported the germination of the zygospores of this species and established the fact that the sporangia arising from these germinations bear spores which are all homothallic. His results indicate that germination usually occurs within two months after the formation of the

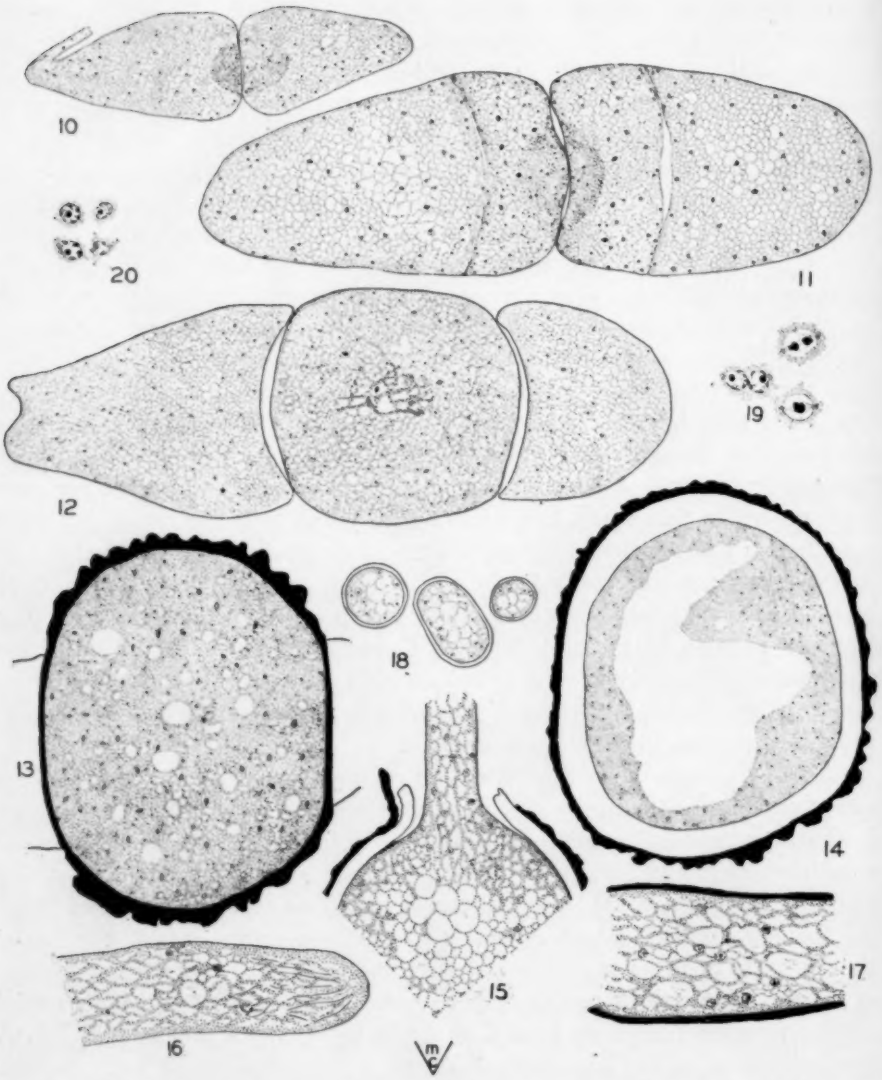

FIG. 10. *Sporodinia grandis*. Progametangia 4 hours old (F.A.A.; Haematoxylin). ×170. FIG. 11. Progametangia 8 hours old, the angular bodies are mucorine crystals (F.A.A.; Cahal-Brozek). ×170. FIG. 12. Coenozygote 10 hours old, the dark material in center of spore represents remnants of progametangial membrane (F.A.A.; Buffer). ×170. FIG. 13. Zygospore 5 days old, mucorine crystals and oil vacuoles present (Flemming's; Haematoxylin). ×170. FIG. 14. Dormant zygospore 12 days old (S.M.C.; Feulgen). ×170. FIG. 15. Portion of germinating zygospore and germ tube 17 days old (Flemming's; Haematoxylin). ×170. FIG. 16. Tip of vegetative hyphae showing threadlike mitochondria and expanded nuclei (Z.R.C.; Haematoxylin). ×660. FIG. 17. Portion of zygospore showing heavy wall and expanded nuclei (Flemming's; Triple). ×660. FIG. 18. Sporangiospores with unexpanded nuclei (F.A.A.; Buffer). ×900. FIG. 19. Metaphase, anaphase, and telophase of mitotic division in young coenozygote (Flemming's; Haematoxylin). ×1500. FIG. 20. Expanded nuclei in coenozygote showing central body and chromatic reticulum (Flemming's; Triple). ×1500.

zygospores, although he points out that it is impossible, on the basis of gross examination, to distinguish between living and dead zygospores. During the course of this study a large number of zygospores of *Sporodinia* were germinated and much information concerning the details of this process accumulated. This will be presented in a subsequent publication. There is very strong evidence that in artificial culture at least the zygospores remain viable for only about a month after their formation, and the greatest number of germinations have been obtained from zygospores about two weeks after the formation of the exospore. At this time it was frequently possible to obtain 100 per cent germination of zygospores isolated under sterile conditions and kept uncontaminated by other organisms. After this critical period has passed, the percentage of germinations fall off rapidly and it has proved impossible to germinate spores over six weeks old. For this reason, it has been assumed that spores over this age are probably no longer viable, although Blakeslee's statement concerning the impossibility of distinguishing living from dead spores externally is fully confirmed. Since many of Keene's data were drawn from spores over six weeks old, it appears probable that she was at times dealing with dead spores, and that certain of the peculiar chromatic bodies which she describes in these "mature" spores were, in reality, decomposition products.

Approximately two weeks after the deposition of the exospore the spore contents become vacuolate and much of the reserve substance present disappears. The nuclei assume the expanded condition, but remain in the peripheral regions of the spore and mitotic divisions commence. A certain amount of swelling of the spores takes place, and externally this stage may be recognized by the mottled appearance of the exospore. By the time the oil reserve has been completely absorbd, the endospore and exospore are ruptured at a point usually close to the median line of the spore and a thick germ tube is pushed out (fig. 15). Mitotic divisions take place rapidly as this tube develops, but they differ in no way from those seen in the vegetative mycelium. Growth of the tube is fairly rapid and in a moist atmosphere it may in the course of 48 hours reach a length of 5 centimeters. After the initial period of growth is over, the tube develops a series of dichotomous branches which in turn produce terminal sporangia. If the primary tube is injured or encounters any obstructions several secondary tubes may be developed, and growth of these proceeds until all the reserve contents of the spore have been utilized. In the growing tubes most of the cytoplasm is aggregated near the tips while the older portions of the tube quickly become vacuolate and develop pseudosepta of the same type as those in the asexual sporangiophores. Harper's account (12) of the development of the vegetative sporangia is fully confirmed by a study of both vegetative and germ sporangia. No peculiarities of mitotic division, and no evidence of nuclear

fusion in either germ tube or germ sporangium have been observed. The spores of the germ sporangium are multinucleate and give rise to homothallic mycelia.

From a consideration of the accounts of Dangeard, Leger, Moreau, Lendner, Keene, and Ling Young the conclusion is reached that nuclear fusions occur in the early stages of zygospore formation. All these authors affirm the difficulty in distinguishing nuclear fusion from nuclear division and have shown that only a slight size difference distinguishes fused from unfused nuclei. Lendner alone has been able to demonstrate typical fusion nuclei, but as pointed out above his interpretation may be questioned. Ling Young has indicated that there is apparently no essential difference between nuclear behavior in azygospores, where nuclei of only one potentiality are present, and in zygospores where presumably there are nuclei of two potentialities. Gruber has not seen any fusions whatever nor has he reported any nuclear degeneration. The present study indicates that the size difference in nuclei at various stages of zygospore formation and also at other stages in the thallus may be correlated directly with the state of activity of the cytoplasm. Expanded nuclei in active cytoplasm always appear larger and more chromatic than unexpanded nuclei in senescent cytoplasm. This situation has not been elucidated in previous studies on the Mucorales. Such a concept offers a very logical explanation of the situation described by Dangeard, Keene, and Ling Young, in which nuclei of two types are present during the young zygospore stages, for certain supernumerary nuclei may, just before degeneration, enter the unexpanded phase. If this hypothesis is valid, then in reality no investigator has ever encountered true karyogamy in *Sporodinia*. That such a situation may be true seems plausible in the light of facts garnered from a study of other members of this group where karyogamy is a clearly defined process. The question therefore arises whether karyogamy regularly occurs in *Sporodinia*, or whether the stimulus of plasmogamy is sufficient to induce an apomictic development and germination of the zygospore. In the present study no indication whatsoever of nuclear fusion or reduction division at any stage in the life cycle has been encountered.

The fact that the expression of sexuality in *Sporodinia*, manifested by the production of zygospores, is very largely dependent upon environmental factors as shown by the researches of Blakeslee (2) and Robinson (24) indicates that the sexual potentiality of this species is not particularly strong when compared with such other homothallic mucors as *Zygorhynchus dangeardi* and *Mucor genevensis* in which zygospore production occurs regularly under almost any environmental conditions. This situation, coupled with the fact that undoubted karyogamy has not been conclusively demonstrated, may further indicate that in *Sporodinia* the zygospore no

longer represents a truly sexual spore but is only a highly specialized type of asexual reproduction retaining externally the ancestral zygosporic form. Such an interpretation requires the assumption that homothallism of this type is a derived condition. The work of Burgeff on *Phycomyces* and Krafczyk (15) on *Pilobolus* has emphasized the fact that the homothallism shown by certain isolates of these genera results from a heterocaryotic condition in the mycelia and depends for its expression on the balance existing between nuclei of opposite potentialities present in any given mycelium. Such homothallism is quite different from the genic homothallism of *Zygorhynchus* and some species of *Mucor* in which the mycelium is homocaryotic and the homothallic condition arises from self-fertility rather than from a balance between nuclei of different genotypes. Furthermore, experiments carried out by Ling Young (18) on mycelium regenerated from the suspensors and young progametangia of *Sporodinia* showed that this mycelium was both homocaryotic and homothallic and was capable of producing normal zygospores, thus indicating that in the initials of the sexual organs there had been no localization of opposed sexual tendencies. Since it has been shown (8) that well-defined karyogamies occur in such species as *Zygorhynchus dangeardi* and *Absidia spinosa* which show this same homocaryotic condition, it seems not unreasonable to suppose that in *Sporodinia* the situation has been carried one step further, and that nuclear fusion has become obsolete. Such a simplification of the life cycle might be expected in a highly specialized semi-parasitic species of this type. The development of the zygospore is then explainable upon the basis of habit derived from the parental homocaryotic form which, in turn, was derived from an originally heterocaryotic, heterothallic condition by the appearance in some strains of a condition of self-fertility in the nuclei. Additional evidence for this situation might be deduced from Lendner's (17) report of a reduced number of karyogamies in a strain of *Sporodinia*, although it has previously been suggested that his conclusions may have resulted from the incorrect interpretation of an artifact. A reduction in the number of karyogamies, from a condition of multiple fusions as seen in *Zygorhynchus* to a condition where only two fusions occur, such as Lendner reports for *Sporodinia*, may well be interpreted as an intermediate step in the progression towards a complete loss of karyogamy. It is perfectly plausible that the nuclear condition may not be stable throughout all the races of the species, and that the material used in this study represents a more advanced condition than that present in Lendner's material.

It is evident that a number of strains of *Sporodinia* from different localities must be investigated in order to ascertain whether the nuclear condition is in a transitional state or whether it has reached a uniform development in a wide range of isolates. These isolates are unfortunately not

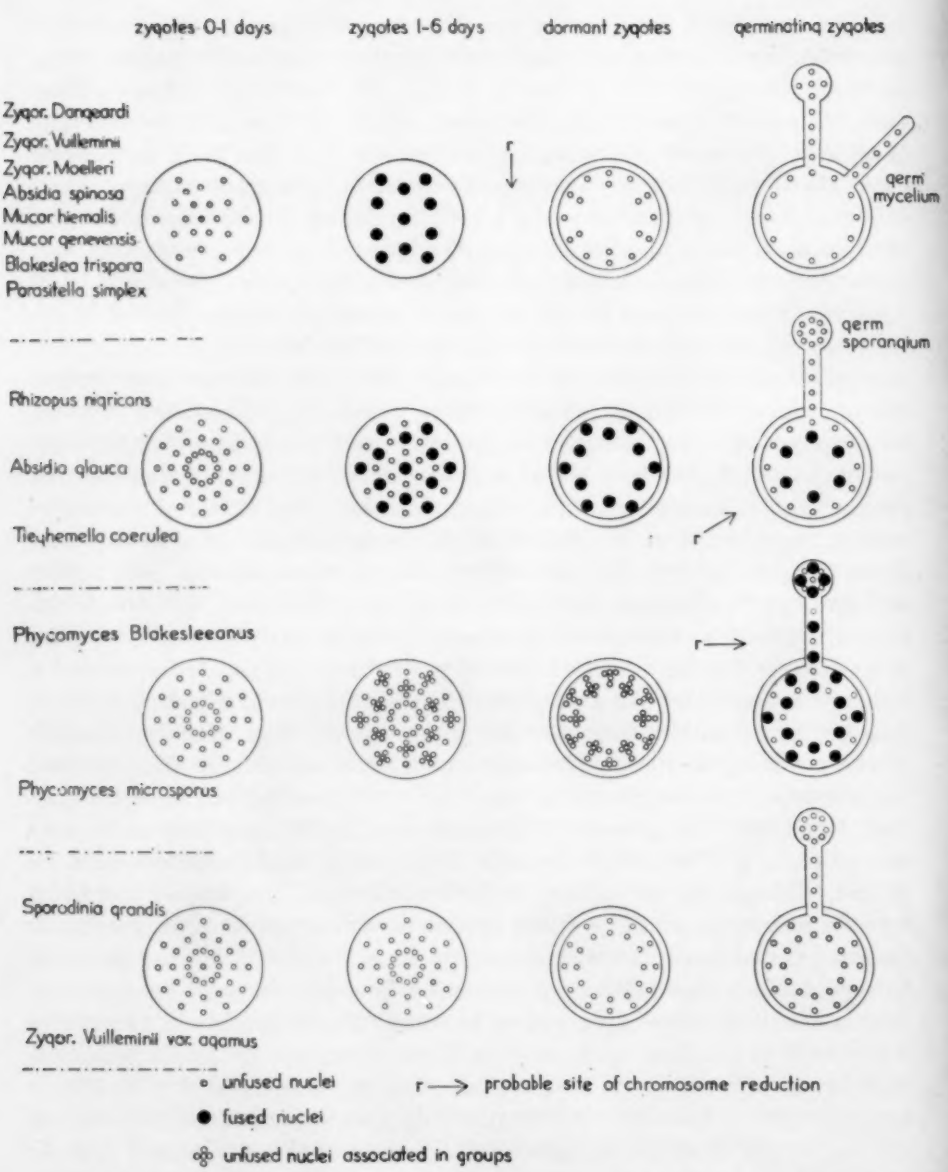

FIG. 21. Diagrams illustrating the probable nuclear condition in the zygotes of the 15 species included in this study. The geometric arrangement of the symbols has no significance except to indicate the approximate distribution of the nuclei at various stages. The arrows indicate the stages at which meiotic divisions presumably occur. The four time intervals given are arbitrary and may vary under different conditions, but merely represent the average intervals at which conspicuous nuclear phenomena occur in the four groups.

available at present. Until undoubted nuclear fusions can be demonstrated, it appears that the development and germination of the zygospores in my material of *Sporodinia* is of an apomictic nature, and in this case plasmogomy furnishes the necessary stimulus to further development ordinarily supplied by karyogamy. The zygospore must then be regarded as a vestigial structure representing the last evidence of an obsolete sexuality.

DISCUSSION

A consideration of the fifteen forms included in this study indicates that four general patterns of development occur. These patterns are illustrated diagrammatically in figure 21. It is possible that further investigation of other species in the order will reveal that all the forms may be grouped according to these general formulae. It is equally probable that still other conditions may exist, or that intergradations between these four basic patterns can be demonstrated. In the species studied here intergrading forms were not observed. Some doubt may arise concerning the correct interpretation of the pattern illustrated by *Sporodinia grandis* and *Zygorhynchus vuilleminii* var. *agamus*. It is evident that the behavior patterns of the nuclei of these forms are not homologous and have arisen in completely different ways. The apomictic development of *Sporodinia* apparently represents the loss of the sexual function of the nuclei, with physiological differences in the plasma, under the influence of external conditions, sufficient to produce a pseudosexual reproductive mechanism. This type of pattern in *Z. vuilleminii* var. *agamus* on the other hand represents a degeneration from the earlier sexual condition caused by a suppression or loss of function of the nuclear complement of one gametangium. That this is an advanced rather than a primitive condition is implied by the fact that on those rare occasions when both gametangia function in zygospore formation the nuclear pattern of the zygote is of the same type as that in the species. It is to be expected that in future work on this problem this fourth category of nuclear behavior will serve as a repository for species in which the loss of sexuality has arisen in several ways, and in this respect it must not be thought of as a natural grouping.

Much further work must be done before any valid conclusions can be drawn on the evolutionary course of these patterns. From this preliminary survey it appears that the *Rhizopus* pattern may have arisen from the *Mucor* pattern by a restriction of karyogamy to certain favored nuclei and a deferment of the meiotic process until the time of germination. This condition is carried further in the *Phycomyces* type in which an association, but no fusion, of nuclei occurs early in the formation of the zygote, the fusion being delayed until the time of germination where it is still restricted to favored nuclei. This condition also appears more specialized than the *Rhizopus* type

in that all the fusion nuclei do not undergo meiosis in the first generation, and that certain nuclei apparently persist throughout the life cycle without undergoing karyogamy. This persistence of unfused nuclei, correlated with only partial meiosis and possible degeneration of fusion nuclei, may indicate the origin of the *Sporodinia* type in which karyogamy is apparently obsolete and unfused nuclei regularly persist throughout the life cycle. These specializations in nuclear behavior can be correlated with a general increase in the size and complexity of the thallus as well as with an increasing tendency for the reproductive structure to be borne upon specialized zygosporic hyphae or zygophores rather than upon apparently undifferentiated vegetative mycelia. Further conclusions do not seem warranted without additional information on transitional types.

It will be noted that the concept of expanded and unexpanded nuclei is of great importance to the interpretation of nuclear behavior in the various stages of the zygote. This concept is equally applicable to fused and unfused nuclei. The numerous reports of nuclear degeneration at various stages in the life cycle, particularly during the dormant periods of the zygospore, are in large part traceable to the failure to distinguish between true nuclear degeneration and the assumption, by persistent nuclei, of the unexpanded phase during periods of cytoplasmic inactivation. In future investigations this distinction should be borne clearly in mind.

The results of this study indicate certain problems which must receive consideration in the future. The most important of these is obviously a further investigation into the process of meiosis in these forms. As yet our knowledge of chromosome reduction is confined to Burgeff's brief discussion of the phenomenon in *Phycomyces blakesleeanus* and the present report of prophase configurations in *Absidia spinosa*. The importance of an understanding of the nuclear patterns described here to phylogenetic studies in this order makes imperative the investigation of other species from the same standpoint. In connection with the apomictic development of the zygospore of *Sporodinia* an investigation of such other semi-parasitic homothallic genera as *Dicranophora* and *Spinellus* may indicate a similar condition. The present study has only partially clarified the nature of the chondriome in the Mucorales, and the origin of the oil plastids and their possible connection with mitochondria and nuclei remains obscure. It is hoped that a further study of these critical phenomena, by the use of more precise techniques, may be instituted in the near future.

SUMMARY

1. The nuclear condition throughout the life cycle of fourteen species and one variety of the Mucorales has been investigated by the use of several fixing and staining techniques not previously applied to this group. The

results obtained with these new methods are compared with those obtained by the usual techniques of fungus cytology.

2. Nuclei are shown to exist in two conditions at various stages in the life cycles. Expanded nuclei occur at all stages where the cytoplasm is in an active state. Unexpanded nuclei are present wherever cytoplasmic activity has slowed down or ceased. The failure to recognize the significance of these two nuclear phases has accounted for several erroneous interpretations in previous investigations.

3. Four patterns of nuclear behavior are described in these 15 forms. In the *Mucor* type all functional zygospore nuclei undergo karyogamy followed by immediate reduction division prior to the onset of dormancy in the zygospore. In the *Rhizopus* type only a portion of the nuclei in the zygospore fuse and the supernumerary nuclei degenerate before the rest period sets in, while reduction division is delayed until the germination of the zygospore. In the *Phycomyces* type the nuclei associate in groups in the young zygospore and persist in this association until the germination of the zygospore. A partial fusion of the nuclei present occurs just prior to germination, but the unfused nuclei do not degenerate. Reduction division of some of the fusion nuclei occurs in the germ tube and the developing germ sporangium, but some of the apparently unreduced diploid nuclei enter the sporangiospores of the germ sporangium. These presumably pass to the next generation in the unreduced condition. In the *Sporodinia* type nuclear fusion apparently does not take place at any stage in the life history and development of the zygospore is apomictic.

4. The possible course of evolution of these patterns is discussed briefly.

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(See also under Ecology: **Camp**)

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